TUL 7704

HARVARD UNIVERSITY

LIBRARY

OF THE

Museum of Comparative Zoology

(Complete in 12 parts)

TULANE STUDIES IN ZOOLOGY

6517
11-3

Volume 1, Number 1 June 1, 1953

ON A NEW GENUS AND SPECIES OF MYSID FROM SOUTHERN LOUISIANA

(CRUSTACEA, MALACOSTRACA)

ALBERT H. BANNER

DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY, UNIVERSITY OF HAWAII, HONOLULU

MUS. COMP. ZOOL.
LIBRARY
JUL 14 1953
HARVARD
UNIVERSITY

TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

FENNER A. CHACE, JR., Curator of Marine Invertebrates, United States National Museum, Washington, D. C.

MRS. WALTER M. TATTERSALL, Pendeen, Sinah Lane, Hayling Island, Hants., England.

GEORGE HENRY PENN, Associate Professor of Zoology, Tulane University of Louisiana, New Orleans, U. S. A.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

Price for this number: $0.25.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University of Louisiana,
New Orleans, U. S. A.

MUS. COMP. ZO
LIBRARY
JUL 14 1953
HARVARD
UNIVERSITY

ON A NEW GENUS AND SPECIES OF MYSID FROM SOUTHERN LOUISIANA[1]

(CRUSTACEA, MALACOSTRACA)

ALBERT H. BANNER,

Department of Zoology and Entomology, University of Hawaii, Honolulu.

Only five species of mysids have been reported from the fresh waters of the Americas (Tattersall, 1951:4; Banner, 1948:72). Three of these are known only from tropical America: *Antromysis cenotensis* Creaser, from the caves of Yucatan; *A. anophelinae* Tattersall, from the holes of a terrestrial crab in Costa Rica; and *Diamysis americana* Tattersall, from ditches in Dutch Guiana. The other two species are found in temperate and arctic North America: *Mysis relicta* Lovén, which reaches south from the arctic coast to the Great Lakes, and which apparently is a circumarctic species; and *Neomysis mercedis* Holmes,[2] which ranges from brackish into fresh waters along the Pacific Coast from California to Alaska. No mysids have been reported before from the fresh water of the Mississippi basin.

TAPHROMYSIS[3], *gen. nov.*

Diagnosis — Body of usual form, carapace covering most of thorax. Eyes well developed. Antennules of normal configuration. Antennal scale rounded and bearing setae on both sides. Labrum rounded anteriorly. Mandibles with strong dentate process laterally on *corpus mandibulae.* Tarsus of thoracic legs (e.g., portion beyond "knee") of four articles. Three pairs of oostegites in females, but those of the sixth thoracic segment strongly reduced. Adult males without sternal thoracic processes. All female pleopods reduced to plates; first and second pleopods of males similar. Third pleopods of males consisting of two articles, representing the protopod and endopod; exopod lacking. Fourth pleopods of males large, with exopod of seven articles, and bearing strong terminal bristles that form a feeble "pincher"; endopod short and composed of two articles. Fifth pleopod of males of two slender articles. Uropods without spines near statocyst. Telson posteriorly cleft.

Type species: *Taphromysis louisianae* Banner.

Discussion — *Taphromysis* was erected solely for the species described below.

This genus plainly belongs to the family Mysidae, the sub-family Mysinae and the tribe Mysini of H. J. Hansen (1910:13), and within

[1] Contribution No. 35, Hawaii Marine Laboratory.

[2] The taxonomy of this species will be discussed in another paper.

[3] Generic name derived from *taphros*, Greek for ditch, referring to the habitat where the type species was found.

the tribe to the *Mysis*-group of Zimmer (1915:202-216). This group may be recognized by a series of characteristics — the lack of an anterior process on the labrum, the possession by the males of six or seven articles in the exopod of the fourth pleopods, and the development on this ramus of long terminal and sub-terminal bristles to form a type of a feeble "pinchers"; and the possession of a truncate or terminally cleft telson. This group until now contained six recognized genera: *Mysis* Latreille, *Hemimysis* G. O. Sars, *Paramysis* Czerniavsky, *Caspiomysis* G. O. Sars, *Schistomysis* Norman and *Synmysis* Czerniavsky. From the last four genera *Taphromysis* is separated by a number of characteristics, the most important being the absence of the exopod on the third pleopod of the males and the presence of setae on the outer margin of the antennal scale.

Taphromysis shows many similarities to *Mysis* and especially to the species *M. relicta* Lovén. If female specimens alone were available to study, only the shorter antennal scale and the presence of the mandibular process could be relied upon to distinguish *Taphromysis.* In the male, however, the exopod of the third pleopod is well developed and consists of six articles in *Mysis* while the entire ramus is lacking in this genus. A difference of this category in the present scheme of classification is considered to be of generic worth.

Taphromysis also shows close affinity to the genus *Hemimysis.* The antennal scale, variable in *Hemimysis,* usually bears setae only on the distal portion of the outer margin instead of along its entire length as in this genus. The presence of the dentate process on the lateral surface of the mandible has not been noted in *Hemimysis.* The oostegites are of similar development in the two genera. In *Hemimysis* the exopod of the third pleopod of the males may be reduced or entirely wanting as it is in this genus. The fourth pleopods of the males are the same in both genera [according to Illig (1950:587), but Tattersall and Tattersall (1951:331) state that the exopod in *Hemimysis* consists of only five to six articles]. The telson in both genera is quite similar. However, the two genera may be distinguished by the fifth pleopods of the males which in *Hemimysis* are well-developed, biramous and natatory, but are reduced to two simple elongate articles in *Taphromysis.*

While this genus appears to lie midway between *Mysis,* to which it is similar in the nature of the fourth and fifth pleopods of the male, and *Hemimysis,* to which it is similar in the nature of the third and fourth pleopods of the male, the modification of the third pleopods appears to be more distinctive than that of the fifth, and the genus, therefore, probably is more closely related to *Hemimysis.* However, it appears to me that these specimens raise doubts as to the validity of small modifications of the antennal scale and of the pleopods of the male as characteristics for generic separations.

It is noteworthy that the American *Taphromysis* should be so closely related to the genus *Hemimysis* which is restricted to the waters of western Europe and the general Mediterranean region,

penetrating into the brackish water of the Black Sea drainage of Rumania (Bacesco, 1940). Tattersall (1951:228) has postulated that the genus *Diamysis,* a brackish water genus with three Mediterranean species — ecologically similar, therefore, to *Hemimysis* — and one American fresh water species, was once a widespread tropical genus of the Tethys Sea of the Tertiary, and that the modern discontinuous distribution represents a relict fauna. It is possible that the genus *Hemimysis* once had a similar distribution, but in the case of its American species the long isolation resulted in sufficient modification to support its classification as a separate genus.

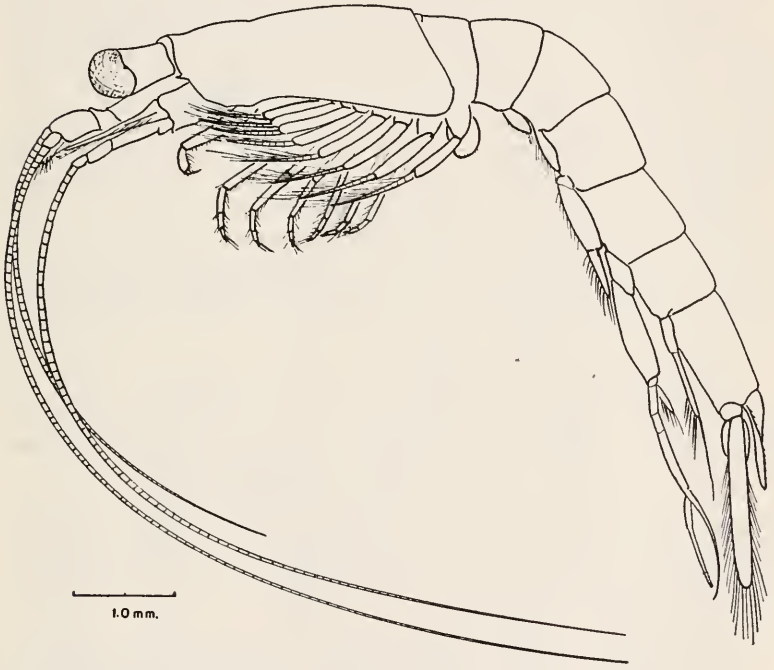


Figure 1. *Taphromysis louisianae,* adult male.

TAPHROMYSIS LOUISIANAE, *sp. nov.*

Type specimens — A male 7.0 mm long, United States National Museum, Catalog No. 94829; paratypic series at the United States National Museum, Catalog No. 94830 and also in Tulane University collection, No. 2643.

Type and paratypes all collected in a roadside ditch at Gueydan, Vermilion Parish, Louisiana, Feb. 2, 1952 by F. F. Vizzi. The water was reported to be fresh and static; the bottom was reported to be mud and the vegetation to be sparse.

Description — Adult females about 8.0 mm long, adult males up to 7.5 mm long.

Body of usual development and proportions. Carapace posteriorly leaving dorsal portion of the eight and part of seventh thoracic segments exposed. Rostral plate short, scarcely reaching the bases of eyes, rounded and depressed. Anterior margin of carapace slightly below base of eyes bearing small acute tooth. Anterior lateral corners of the carapace rounded.

Eyes somewhat elongate and sub-cylindrical, with total length twice maximum breadth of stalk and with evenly rounded corneas 0.4 length of entire stalk. No ocular papilla.

Antennular peduncle with end of second article reaching slightly beyond end of eyes. Basal article 2.7 times length of second and 2.0 times length of third articles. No article bearing any conspicuous teeth or denticles. *Process masculinus* well developed, 1.4 to 2.0 times length of third antennular article, and bearing fine setae. Outer flagellum slightly longer than body, inner flagellum about half body length.

Basicerite of antenna bearing small lateral tooth. Scale reaching to end of antennular peduncle, about 4.6 times as long as broad, bearing setae on both sides; tip rounded; distal twentieth demarked by feeble articulation. Carpocerite of antennal peduncle reaching past middle of scale. Flagellum as long as outer antennular flagellum.

Labrum of normal form, anteriorly rounded.

Opposing faces of mandibles with usual development (rows of spines imperfectly shown in drawings because of the rotation of appendage). *Corpus mandibulae* with strong acute denticle laterally directed. Palp normal, maxillules and maxillae normal.

First thoracic leg (maxilliped) with exopod and endopod located relatively close together on the protopod, but not adjacent. Endite of basis and two basal articles of endopod of moderate development. Exopod only slightly shorter than that of second leg. Second thoracic leg also of normal development.

Third to eighth thoracic legs with basis somewhat enlarged; tarsus (or portion beyond "knee") of four articles, including the "end-claw"; penultimate article bearing heavy spine, more than twice as long as end-claw. All exopods well developed with outer distal angle of basal plate sub-acute and not bearing accessory denticles.

Penis lobes of males well developed. Females bearing three pairs of oostegites, with those of sixth thoracic legs reduced to small setiferous lobes.

All pleopods of females reduced to uniramous plates. First and second pleopods of males similar to female pleopods. Third male pleopod with enlarged protopod, exopod entirely lacking, endopod longer than protopod but less than half as broad, consisting of a single article. Protopod and endopod bearing setae.

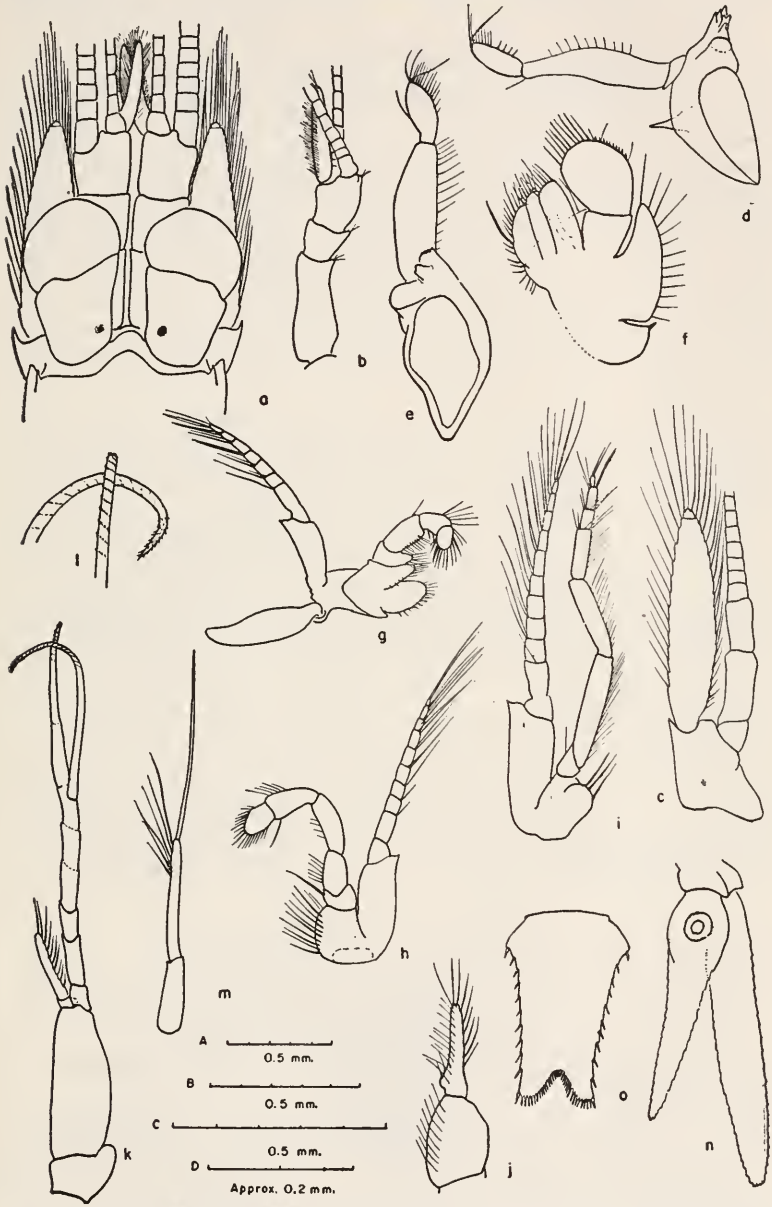


Figure 2. *Taphromysis louisianae,* adult male. **a,** anterior body region, dorsal aspect; **b,** antennular peduncle, medial aspect; **c,** antennal peduncle and scale, ventral aspect; **d,** mandible, posteromedial aspect; **e,** mandible, medial aspect; **f,** maxilla; **g,** first thoracic leg; **h,** second thoracic leg; **i,** seventh thoracic leg; **j,** third pleopod; **k,** fourth pleopod; **l,** tips of distal setae of fourth pleopod; **m,** fifth pleopod; **n,** uropod; **o,** telson. (Figures **d** and **e,** scale B; figure **f,** scale C; figure **l,** scale D; all other figures scale A.)

Fourth pleopod of males very elongate, reaching to distal tip of uropod. Basal article of protopod with heavy but short lobe on outer side. Second article reaching beyond end of fifth abdominal segment. Endopod consisting of two articles, basal only one seventh as long as distal and bearing small exite; distal article reaching beyond second article of exopod and bearing numerous setae. Exopod composed of seven articles, with the articulations between them very faint. Penultimate article bearing a curved spine, as long (if straightened) as the exopod to its base; bearing distally a series of spiral reinforcements and a series of extremely fine spinules on its acute tip. Terminal article fused with strong terminal seta, more blunt and straight but slightly shorter than penultimate setae, distally armed with very fine spinules in diagonal bands. Terminal and subterminal setae forming a feeble "pincher."

Fifth pleopod of male with tip reaching almost to end of sixth abdominal segment, composed of two articles, the distal about 1.5 times length of proximal. Setae found only on distal portion of second article; terminal setae as long as appendage.

Telson short, less than 0.9 as long as sixth segment, broad and distally emarginate. Tip about 0.6 as broad as base, and 0.4 as broad as telson is long. Lateral margins concave and bearing 10 pairs of movable spines. Posterolateral spines not longer than lateral spines. Terminal emargination less than 0.2 length of telson, rounded and "U" shaped, and bearing about twenty pairs of long narrow denticles that are not articulated.

Uropods slightly less than twice as long as telson, of usual form and not bearing any spines near statocyst.

Specimens in preservative without color but bearing a limited number of small stellate melanophores, one middorsally on each abdominal segment, a pair on base of telson, several pairs on ventral side of cephalothorax and its appendages, and two pairs on oostegites.

REFERENCES CITED

Bacesco, M. 1940. Les Mysidaceas des eaux Roumaines . . . *Univ. de Jassy., Ann. Sci.*, 2nd Ser., 24(2): 453-804.

Banner, A. H. 1948. A taxonomic study of the Mysidacea and Euphausiacea (Crustacea) of the Northeastern Pacific. Part II. . . . *R. Canad. Inst., Trans.*, 27(57): 65-125.

Hansen, H. J. 1910. The Schizopoda of the Siboga Expedition. *Siboga-Exped.*, 37: 1-123.

Illig, G. 1930. Die Schizopoden der Deutschen Tiefsee-Expedition. *Wiss. Ergebn. Deutschen Tiefsee-Exped.*, 22(6): 399-625.

Tattersall, W. M. 1951. A review of the Mysidacea of the United States National Museum. *U. S. Natl. Mus., Bul.*, 201: x +292.

Tattersall, W. M. and O. S. Tattersall. 1951. *British Mysidacea*, viii +460. Ray Society, London.

Zimmer, C. 1915. Die Systematik der Tribus Mysini H. J. Hansen. *Zool. Anz.* 46: 202-216.

TULANE STUDIES IN ZOOLOGY

Volume 1, Number 2 July 3, 1953

A CONTRIBUTION ON THE LIFE HISTORY OF THE LIZARD *SCINCELLA LATERALE* (SAY)

RICHARD M. JOHNSON

DEPARTMENT OF BIOLOGY, TENNESSEE WESLEYAN COLLEGE, ATHENS, TENN.

MUS. COMP. ZOÖL. LIBRARY

AUG 24 1953

HARVARD UNIVERSITY

TULANE UNIVERSITY

NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

HOBART M. SMITH, Associate Professor of Zoology, University of Illinois, Urbana.

HENRY S. FITCH, Associate Professor of Zoology, University of Kansas, Lawrence.

FRED R. CAGLE, Professor of Zoology, Tulane University of Louisiana, New Orleans.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost. Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

Price for this number: $0.75.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University of Louisiana,
New Orleans, U. S. A.

A CONTRIBUTION ON THE LIFE HISTORY OF THE LIZARD *SCINCELLA LATERALE* (SAY) [1]

RICHARD M. JOHNSON [2]
Department of Biology, Tennessee Wesleyan College, Athens, Tenn.

The objectives of this research were threefold: to determine size at sexual maturity, the seasonal reproductive cycle, and the reproductive potential of the scincid lizard *Scincella laterale* (Say). Data to accomplish these objectives were obtained by laboratory examination of fresh and preserved material, the latter from the research collections of the Department of Zoology of Tulane University.

Blount (1929), Breckenridge (1943), and Reynolds (1943) present data obtained from histological examinations of gonads of *Phrynosoma solare, Eumeces s. septentrionalis* and *Eumeces fasciatus* respectively. Each of these lizards exhibits essentially the same morphological and physiological sequences of the gonads. The appearance of spermatozoa in January and February is associated with growth of the testes to maximal size; spermatozoa are present in the gonadal ducts through August; disappearance of spermatozoa is concurrent with regression of testes to minimal size in October and November. The ovaries follow the same sequences except for a more rapid enlargement in early spring and a more sudden regression in late summer. *Scincella laterale* parallels the above lizards as regards these phenomena.

MATERIALS AND METHODS

Four hundred and sixty-two specimens (229 males, 233 females) were examined during this investigation. The majority of the specimens had been preserved prior to this study.

Klauber (1943: 20) discusses shrinkage of linear dimensions of snakes in preservative. As a standard procedure is observed for entering specimens in the Tulane University collections, it is assumed that the amount of shrinkage for the same parts of different individuals was the same, if any. If such an assumption is true, then experimental error would not be significant (Simpson and Roe, 1939).

Data obtained from each lizard were: measurements of axilla-groin and snout-vent lengths to the nearest 0.1 mm; counts of dorsal and midbody scale rows as prescribed by Smith (1946: 27, 29, 30); counts and measurements of ovarian follicles and oviducal eggs; the absence or presence of spermatozoa in the testes and/or epididymis and vas deferens.

[1] The generic name *Scincella* follows the nomenclature of Mittleman (1950).

[2] A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science of the Graduate School of Tulane University.

LIBRARY
AUG 24 1953
HARVARD
UNIVERSITY

Testes and gonadal ducts were crushed on a slide and examined under a compound microscope. Filamentous structures converging from the periphery to the center of seminiferous tubules were interpreted as tails of spermatozoa. Tadpole-like structures in the epididymis and vas deferens were accepted as evidence of mature spermatozoa. The presence of spermatozoa in either the testes or gonadal ducts was accepted as a criterion of sexual maturity (Cagle, 1948a: 108; 1948b: 1). Sexually active males are those containing spermatozoa in the epididymis and vas deferens (Cagle, 1948b: 1).

Measurements of ovarian follicles and oviducal eggs were obtained with an ocular micrometer. The former were measured for greatest diameter, the latter for greatest length and width. After being measured each egg was opened for inspection. All oviducal eggs observed during this study were enclosed in leathery shells with fine longitudinally oriented striations.

Tail lengths were used in the study of sexual dimorphism of males and females of series Tulane 14108. Only tails showing no interruption of symmetry of scalation, except for deletion of scale rows, and not showing signs of regeneration were considered. Because of the high frequency of incomplete or regenerated tails in series Tulane 14108, this measurement was subsequently abandoned.

Of the 32 males and 37 females in this series, 20 males (62.5%) and 23 females (62.2%) had broken or regenerated tails. There was no indication of correlation between snout-vent length and the frequency of tail injury. The loss of the tail may be ascribed to injury as a result of contact with members of the same species (Carr, 1940; Lewis, 1951) and/or predation. This author has observed captives of *Scincella* seize and attempt to eat the tails of cage mates.

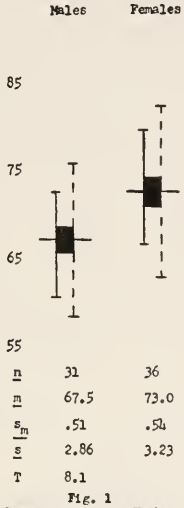
To obtain estimates of growth rates, size groups of 4 mm were selected. The range between minimum and maximum snout-vent lengths of hatchlings was 4 mm. The bias of collecting and possibly the method of selecting size classes may introduce error in the estimate of growth rate.

The method of plotting Figures 1-5, 7-10, is adapted from Cazier and Bacon (1949). In these figures the horizontal bar is the mean, the solid rectangle is the mean plus-and-minus three standard errors, the dashed line the mean plus-and-minus three standard deviations, and the solid line the range of observations. Abbreviations and statistical symbols employed are: b, regression coefficient; m, sample mean; n, number of observations; s, standard deviation; s_m, standard error (Snedecor, 1946); T, value of significance of difference between any two statistics (Peatman, 1947).

SEXUAL DIMORPHISM

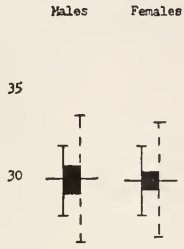
Series Tulane 14108 from Bonnet Carré Spillway, St. Charles Parish, Louisiana, collected February 12, 1950, was used as the standard to determine sexual dimorphism. The following data were employed:

snout-vent lengths; axilla-groin/snout - vent length; snout - vent/tail



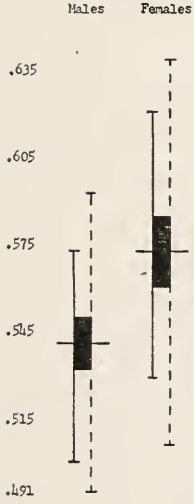
	Males	Females
n	31	36
m	67.5	73.0
s_m	.51	.54
s	2.86	3.23
T	8.1	

Fig. 1
Comparison of the Number of Dorsal Scale Rows of Tulane Series 14108.



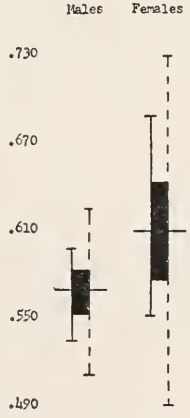
	Males	Females
n	29	36
m	30.1	30.0
s_m	.22	.18
s	1.20	1.07
T	0.00	

Fig. 2.
Comparison of the Number of Midbody Scale Rows of Series Tulane 14108



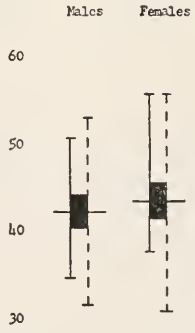
	Males	Females
n	32	37
m	.543	.574
s_m	.003	.004
s	.017	.022
T	6.2	

Fig. 3.
Comparison of Axilla-Groin/Snout-Vent Ratios of Series Tulane 14108.



	Males	Females
n	12	14
m	.570	.612
s_m	.005	.011
s	.019	.040
T	3.5	

Fig. 4.
Comparison of Snout-Vent/Tail Length Ratios of Series Tulane 14108.



	Males	Females
n	32	37
m	42.7	43.8
s_m	.63	.67
s	3.58	4.06
T	1.3	

Fig. 5.
Comparison of Snout-Vent Lengths of Series Tulane 14108

length; dorsal and midbody scale row counts. Pigmentation of the gular region and lower labials was also studied.

These males and females differ significantly [T greater than 2.5 (Peatman, 1947)] with respect to dorsal scale row counts, axilla-groin/snout-vent length ratios, and snout-vent/tail length ratios (figs. 1, 3, 4). The larger values for dorsal scale row counts and axilla-groin/snout-vent length ratios for females might be correlated with capacity for egg production as suggested for snakes by Blanchard (1921: 6) and Ortenburger (1928: 10-11). The males and females did not differ significantly with respect to midbody scale row counts and snout-vent lengths (figs. 2, 5), but the females possessed the greatest snout-vent length. All of these specimens are 35 mm or more in snout-vent length. It is evident that sexual dimorphism does exist for specimens of this size with males having fewer dorsal scale rows, smaller axilla-groin/snout-vent ratio, and smaller snout-vent/tail length ratio (*i. e.,* longer tails).

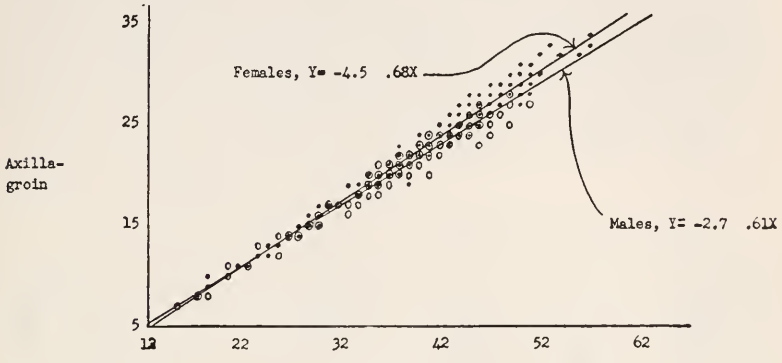
Identification of sex, verified by dissection, is not possible on the basis of pigmentation. Gular pigmentation is most intense in those individuals having the darkest overall coloration.

Klauber (1937: 12, 16; 1943: 31) has shown sexual dimorphism to exist in juveniles of certain species of snakes. To test for sexual dimorphism in juvenile *Scincella,* a series of 16 males and 8 females less than 35 mm snout-vent length were utilized. As discussed below, 35 mm snout-vent length is the lower limit of sexually mature individuals. The males ranged from 16.5 mm to 34.8 mm, the females from 18.9 mm to 34.8 mm. For the character of axilla-groin/snout-vent length ratio these males and females could be considered significantly different, T=2.4; males: m, .489, s_m, .003; females: m, .526, s_m, .003. The T-value is probably high as a result of the small numbers of individuals compared and of the difference in average age as indicated by the difference in average snout-vent lengths; males: m, 22.4 mm, s_m, .45 mm; females; m. 27.2, s_m, .66 mm; T=2. Sexual dimorphism is shown in figure 6 to begin at about 24 mm snout-vent, but is not definitely shown by the series under discussion. Rather, this series may show changed body proportions in young of different age groups. The inclusion of nearly mature individuals in the upper limits of snout-vent length may also contribute to this apparent difference (Klauber, 1943). These males and females differed significantly as regards dorsal scale counts: male, m, 68; females: m, 74, T=3.3, but not from the counts of males and females respectively of series Tulane 14108. They did not differ significantly from each other, nor from males and females of the latter series, as regards midbody scale row counts.

Coefficients of regression of axilla-groin on snout-vent of 66 males and 85 females are .93 and .98 respectively (fig. 6). Lewis (1951) and Smith (1946) do not give criteria for distinguishing sexes.

Descriptions of *Scincella* refer to it as a smooth-scaled lizard. Scales

on the sides of the neck, ventrolateral body surfaces, posterior limb surfaces, and the basal tail region each possess three to four small keels. A few specimens also have keels on the dorsal scales. No keels



	Males ♂		Females	
	Axilla-groin	Snout-vent	Axilla-groin	Snout-vent
n	66		85	
m	19.8	37.1	22.8	40.4
s_m	.65	1.04	.72	1.04
s	5.29	8.48	6.60	9.58

Fig. 6.
Correlation of Axilla-Groin to Snout-Vent Lengths of Males and Females

occur on the scales of the venter. The sexes cannot be distinguished by the absence, presence, or distribution of these keels. The only correlation suggested was with age. The smallest individuals possess the most conspicuous keels and are most frequently the individuals with keeled dorsal scales.

GEOGRAPHIC VARIATION

The wide distribution of *Scincella* offers the possibility for geographic subspeciation (Smith, *op. cit.*). Mittleman (1947) considers the Mississippi River and Lake Pontchartrain in Louisiana as a line of demarcation between subspecies of the salamander *Manculus quadridigitatus*. Samples of *Scincella* from selected areas within the state were compared for possible geographic variation in certain morphological characters.

Three groups of specimens were compared. These were selected for homogeneity of size class, sex, and locality of collection. The 69 specimens, series Tulane 14108, described above were used as the standard to represent central Louisiana. A series of 25 males and 22 females from Grand Isle, Jefferson Parish, and Plaquemines Parish, was selected to represent southern Louisiana. Fourteen males and 11 females from adjacent parishes north of Lake Pontchartrain were selected as the northern sample. These series were compared, sexes separately,

with respect to axilla-groin/snout-vent length and dorsal scale row counts (figs. 7-10) and midbody scale rows. Tests for significance of difference were negative for these characters among the three regions. Midbody scale row counts, means plus-and-minus three standard errors, of the northern and southern samples, [males, 29.1±.32 and 29.4±.27 respectively, and females, 29.2±.30 and 30.2±.37 respectively] are well within the limits of the males and females of series Tulane 14108

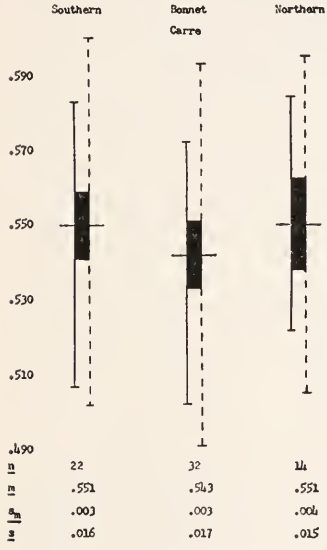


Fig. 7.
Comparison of Axilla-Groin/Snout-Vent Length Ratios of Three Series of Males.

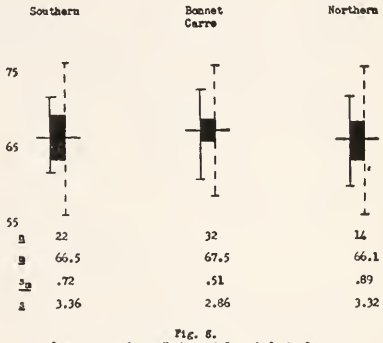


Fig. 8.
Comparison of the Number of Dorsal Scale Rows of Three Series of Males.

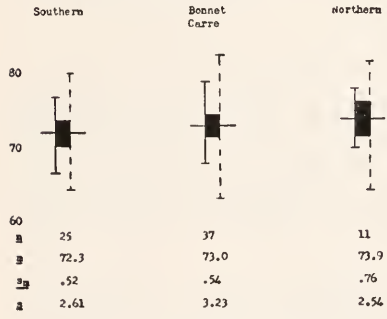


Fig. 10.
Comparison of the Number of Dorsal Scale Rows of Three Series of Females.

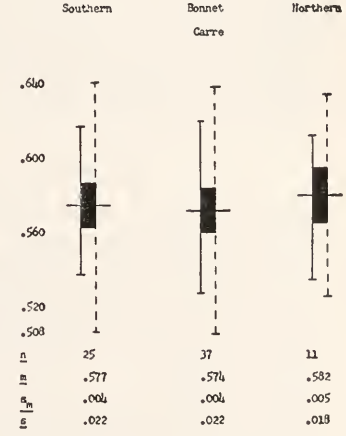


Fig. 9.
Comparison of Axilla-Groin/Snout-Vent Length Ratios of Three Series of Females.

(fig. 2). Lewis, *op. cit.*, lists 30 midbody scale rows and 61-71 dorsal scale rows for Texas specimens. These counts are in agreement with Louisiana specimens if the counts of the dorsal and midbody scale rows of males and females are combined.

Coloration was of no value in these comparisons as it is difficult to evaluate and showed no subjective geographic variation. Specimens from all three areas could be matched as regards extremes of intensity and color pattern.

As regards the morphological characters studied, the Louisiana *Scincella* may be considered as a single form. Thus, series of lizards from various parts of the state may be combined for purposes of this study. As there is a decided difference in the ecology of northern and southern Louisiana (Viosca, 1933), the possibility of physiological differences remains (Mayr, 1942).

SEXUAL MATURITY AND SEASONAL ACTIVITY

Males contained mature spermatozoa in the testes at a minimum class range of 32-35 mm (actually 35 mm) snout-vent length (fig. 11). Spermatozoa are present in the testes and/or gonadal ducts from January through August. Sexual activity thus prevails for eight months of the year. The absence of spermatozoa from the ducts, but their presence in the testes, of individuals in the lower class limits in February and March indicates that these individuals are entering their first season of sexually maturity. Complete absence of spermatozoa in the sexually mature size group individuals during the breeding season (January through August) occurred in only four instances. A February specimen is probably immature. The other three, two in March in the 40-47 mm size groups, one in August in the 44-47 mm size group, may be senile or otherwise physiologically incapacitated. The August specimen may have exhausted its spermatozoa. Spermatozoa are absent from all individuals of the sexually mature size groups from October to December. There are too few specimens from the month of September for any assumptions.

On the basis of the presence of oviducal eggs, the minimal size group for sexually mature females is 40-43 mm (actually 40 mm). Only two instances (December) of ovarian follicles equal to or greater than 1 mm in diameter are present during the period of sexual inactivity of males (October through December). On the basis of possessing follicles of 1 mm or more in diameter during the breeding season (*cf.* discussion of reproductive potential) females may be considered mature. The minimal size group exhibiting this criterion is 36-39 mm snout-vent. No individuals less than 35 mm snout-vent possessed follicles of this diameter at any time during the year. The presence of follicles of this diameter coincides with the presence of spermatozoa in the vas deferens of males. Oviducal eggs are present during the months of March through August, indicating potential egg deposition for those months. Literature reports of earliest dates for oviducal eggs are March 25, Mississippi (Cook, 1943: 19) and April 7, Texas (Lewis, *op. cit.*).

Assuming copulation to be concurrent with the presence of spermatozoa in the vas deferens and of ovarian follicles of 1 mm or more in

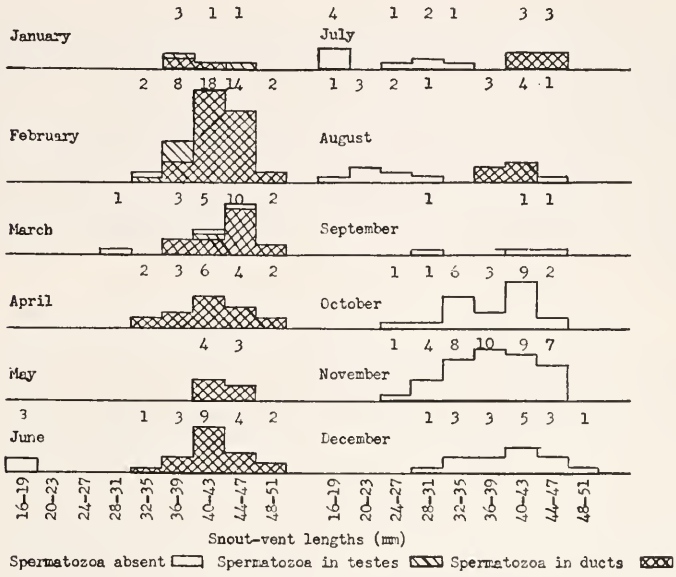


Fig. 11.
Seasonal Distribution of Males

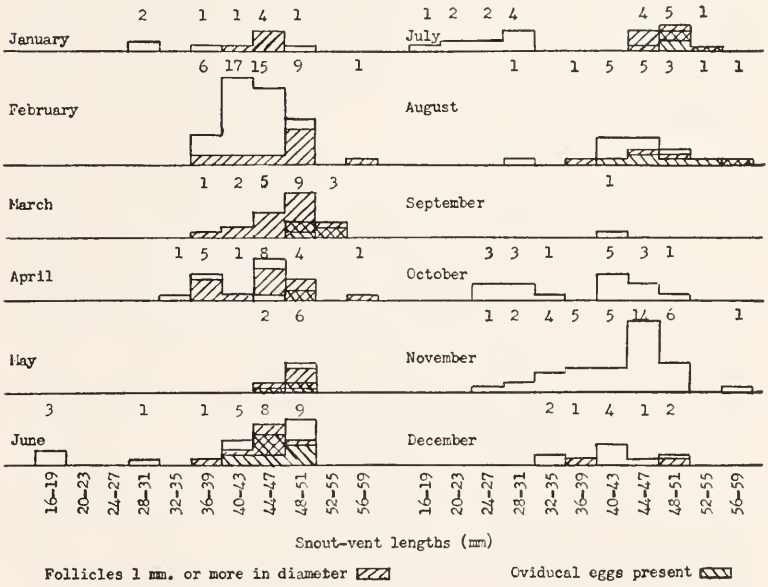


Fig. 12.
Seasonal Distribution of Females

diameter, a time lapse is indicated between copulation and ovulation (figs. 11, 12). It is established that copulation and ovulation are not concurrent in other reptiles (Blount, 1929; Breckenridge, 1943; Cieslak, 1949). Breckenridge, *op. cit.,* reports 35 days as the time between the last observed copulation and the first appearance of eggs. He does not specify oviducal or deposited eggs.

Only one instance of possible copulation was observed in the field. Copulation was not observed in the laboratory. On July 25, 1950, two *Scincella* were discovered beneath a board in a position similar to that pictured for *E. s. septentrionalis* (Breckenridge, *op. cit.,* 596). The position was retained for approximately 30 seconds after their discovery before they separated and ran into the grass. Reports of copulation were not found in the literature.

The earliest date for field collected eggs in Louisiana is May 12 (for this study), and is the earliest known date for any region. The latest date for field collected eggs in Louisiana is July 23. The occurrence of oviducal eggs in August indicates possible deposition in September in Louisiana. Cook, *op. cit.,* and Lewis, *op. cit.,* record clutches for August in Mississippi and Texas respectively.

REPRODUCTIVE POTENTIAL

Determination of the number of broods per female per season requires examination for oviducal eggs and of ovarian follicles. There was a total of 31 females with oviducal eggs from March through August. Two contained eggs only in the right oviduct. No female had eggs only in the left oviduct. The range of numbers of eggs per female was from one to five (two eggs in the left oviduct, three eggs in the right). The average number, plus-and-minus one standard error, of eggs for the right and left oviducts respectively is $1.9 \pm .06$ and $1.5 \pm .05$. This difference is significant, $T = 5.1$. The average number of eggs per female is $3.3 \pm .05$. The range of numbers of eggs per clutch recorded in the literature is from one to five.

A significant correlation of number of eggs to snout-vent length per female does not exist, $b = .069$ (fig. 13). Neither is there a correlation between average egg length and snout-vent length (fig. 14).

During the months of October through December, only two females contained ovarian follicles of a maximum diameter of 1 mm or more. Each of these individuals was collected in December. A female 49.3 mm snout-vent had follicles 1.09 mm and 1.13 mm in diameter; a female 38.8 mm snout-vent had a follicle 1.01 mm in diameter. (The follicle diameters above and subsequently reported are the maxima of left and right ovaries.) The maximum diameter of a follicle of a sexually mature female for October was 0.92 mm. The smallest follicle of maximum diameter of a female of sexually mature snout-vent length was 0.57 mm (November). The smallest female, 27.2 mm snout-vent, collected in November had a maximum follicle diameter of 0.50 mm. The average maxima, October, November, De-

cember, follicle diameters (right and left maxima combined) were: 0.79 mm, 0.80 mm, and 0.94 mm respectively for females 35 mm or more snout-vent, and 0.59 mm, 0.66 mm, and 0.85 mm respectively

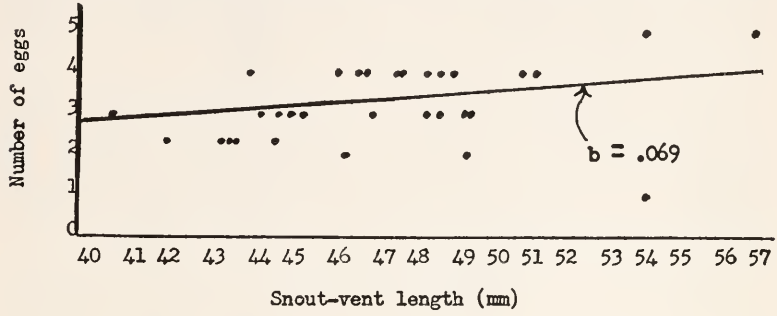


Fig. 13.
Correlation of Numbers of Oviducal Eggs with Snout-Vent Lengths

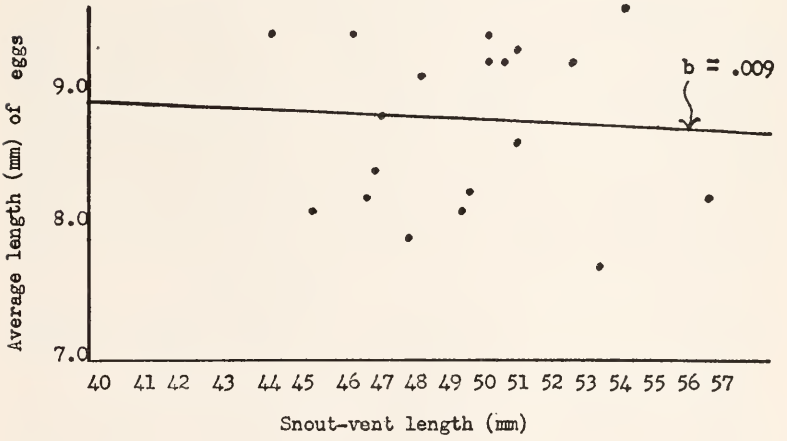


Fig. 14.
Correlation of Average Lengths of Eggs with Snout-Vent Lengths.

for females less than 35 mm snout-vent. The greater monthly average increase in follicle diameter for the latter group of females is probably a reflection of the approach of larger individuals to sexual maturity. Data are too few for September and January.

February collections contained no individuals with oviducal eggs, but the largest follicle diameters were observed among these individuals.

The largest follicles observed for February were in females 50.9 mm and 51.4 mm snout-vent. Respectively, these follicles were: 3.90 mm, 4.23 mm, and 4.50 mm, 4.66 mm in diameter. Presumably these are near ovulation. The smallest maximum follicles observed in sexually mature females were: 0.74 mm, 0.88 mm, and 0.77 mm, 0.92 mm respectively in females 38.9 mm and 39.8 mm snout-vent. The average maximum follicle diameter for February was 1.33 mm. No females less than 35 mm snout-vent were available for study.

March, April, and May are treated together because only one individual less than 35 mm snout-vent is present (April) and because oviducal eggs were present. The largest follicles (March) were those of two females 49.0 mm and 52.0 mm snout-vent. Respectively, these follicles were: 4.77 mm, 4.43 mm and 3.20 mm, 3.47 mm. One female contained two eggs in each oviduct. This female, 49.9 mm snout-vent, had the following follicle diameter maxima: 1.91 mm, 1.79 mm, 1.57 mm, and 3.70 mm, 3.05 mm. The smallest follicle diameter maxima for March were: 0.88 mm, 0.84 mm (female, 45.5 mm) and 0.80 mm (female, 49.8 mm). For April, the largest follicles were: 3.48 mm, 3.58 mm (female, 40.1 mm). The smallest follicle maxima for April were: 0.78 mm, 0.80 mm (female, 34.8 mm). Two females (47.8 mm and 50.6 mm snout-vent) contained oviducal eggs in April. Respectively, their follicle maxima were: 1.01 mm, 1.05 mm and 1.32 mm, 1.30 mm. Follicle diameter maxima for May were: 3.50 mm, 3.68 mm (female, 47.8 mm). Two females collected in May had oviducal eggs and had the following follicle diameter maxima: 1.27 mm, 1.34 mm (female, 49.4 mm) and 1.09 mm, 1.16 mm (female, 46.6 mm). The smallest follicle maxima were those of the latter female above. The average follicle diameter maxima for March, April, and May respectively, were: 1.60 mm, 1.68 mm, and 3.09 mm.

In the June, July, and August collections, four, four, and two females respectively contained oviducal eggs. These females had the following follicle diameter maxima: 2.12 mm, 2.22 mm (female, 44.9 mm), 1.72 mm, 1.76 mm (female, 47.0 mm), 2.49 mm, 2.52 mm (female, 44.3 mm), 1.76 mm, 1.91 mm (female, 46.3 mm) for June; 1.26 mm, 1.42 mm (female, 45.2 mm), 2.59 mm, 2.66 mm (female, 50.8 mm), 3.10 mm, 3.26 mm (female, 48.2 mm), 1.15 mm, 1.26 mm (female, 53.7 mm) for July; 2.20 mm, 2.29 mm (female, 56.8 mm), 1.11 mm, 1.15 mm (female, 52.2 mm) for August. The largest follicle diameter maxima for females not containing oviducal eggs were.—June: 5.07 mm, 5.15 mm (female, 44.2 mm); July: 3.62 mm, 3.77 mm (female, 45.3 mm); August: 3.24 mm, 3.33 mm (female, 47.2 mm). The smallest maximum follicle diameters for sexually mature females were.—June: 1.42 mm, 1.62 mm (female, 39.2 mm); July: 1.43 mm, 1.63 mm (female, 43.6 mm); August: 0.80 mm, 1.59 mm (female, 37.2 mm). The largest maximum follicle diameter for females less than 35 mm snout-vent were.—June: no data; July: 0.34 mm, 0.38 mm (female, 28.7 mm); August: 0.19 mm (female, 29.2 mm). The smallest follicle diameter maxima

for females of this group were.—June: no data; July: 0.19 mm (female, 22.5 mm); August: 0.19 mm (female, 29.2 mm). The average maximum follicle diameters, exclusive of females with oviducal eggs, for sexually mature females were.—June: 2.51 mm; July: 3.00 mm; August: 1.97 mm.

From the above data it is concluded that the egg laying season extends from March or April at least through August, reaching its peak in May, June, and July. Cagle (1948b) reports a similar prolonged period for *Anolis* in Louisiana. As the largest follicles observed were 5.15 mm and 5.07 mm in diameter, it is assumed that ovulation occurs when follicles approach this diameter. The absence of follicles of 1 mm or more in diameter during the months of October and December (except for two individuals, as noted above), but their presence during other months of the year, is presumptive evidence that such follicles are either ovulated or resorbed during the season of their occurrence. The fact that no females less than 35 mm snout-vent possessed follicles of this diameter at any time during the year, and especially during the breeding season, is the basis for using the criterion of follicles equal to or greater than 1 mm in diameter as evidence of sexual maturity. That occassional females may contain oviducal eggs and follicles of 2 mm and more in diameter suggests the possibility of such females having two broods per season. Futher study is necessary to establish this point. Atsatt (1953: 59) cites several distinct clutches in one season for the dwarf chameleon *Microsaura pumila pumila* (Daudin).

Hatchlings are first in evidence in June (figs. 11, 12). These individuals are in the 16-19 mm snout-vent size group. Davis (1945: 116) gives 21 mm (total length minus tail length) as the average snout-vent length of three hatchlings. All individuals of this size group contained remnants of the yolk sac. The absence of this size group in other months of the breeding season does not support the contention of two broods per season. There absence probably reflects the bias of collecting methods rather than the activities of the lizards.

Examination of the oviducal eggs disclosed the presence of an advanced embryo in each of 30 eggs of 10 females collected in March, June, July, and August. The embryos ranged from 1.54 mm to 3.10 mm in length. All were in the somite stage with brain and tail flexures. Weekes (1927a; 1927b) reports ovoviviparity for Old World species of *Lygosoma*.

GROWTH

Conclusive data for determination of growth rate are not available (figs. 15, 16). An estimate of growth rate is necessary to postulate age at which sexual maturity is attained. Except for a male in March and one female each in January and April, all individuals collected from January through May are of adult size (figs. 11, 12). From June through August three size groups are present: hatchlings, sexually

mature individuals, and an intermediate size group. This intermediate size group may be explained by one or both of two causes.

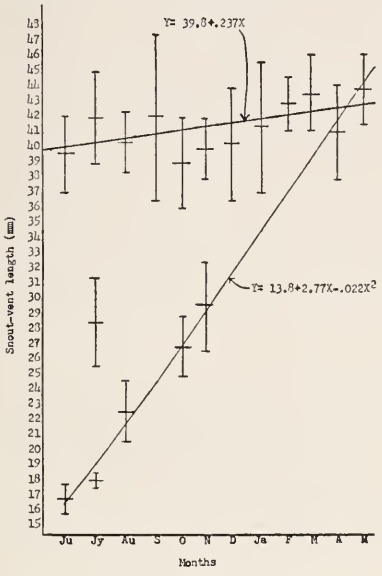


Fig. 15.
Correlation of Snout-Vent Lengths (Means ± Three Standard Errors) With Months (Males).

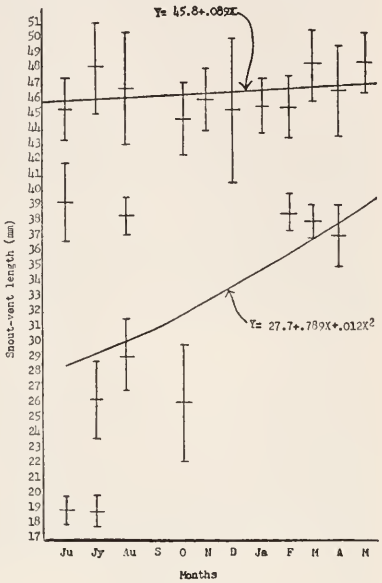


Fig. 16.
Correlation of Snout-Vent Lengths (Means ± Three Standard Errors) With Months (Females).

As mentioned above, no literature records of eggs collected in the field (or laboratory) prior to May were found. Inferring a minimum of four weeks for incubation (the interval from the date of earliest field collected eggs and the appearance of hatchlings), the intermediate size group is best explained as second brood or late single brood individuals of the previous season. These are immature yearlings. That this intermediate size group constitutes early (prior to May or June) hatchlings of the current season is a second less plausible explanation. In either event, most individuals from 24-25 mm snout-vent present in June (?), July, and August would not contribute to the current breeding population.

The distinct size groups present from June through October merge by November and constitute a single group with wide range of snout-vent length measurements. The individuals in the lower snout-vent length classes would be composed primarily of the current season's hatchlings. Late hatchers of the previous season cannot be distinguished. By January the limits of the snout-vent length measurements have been decreased as a result of the increase to mature snout-vent length size of the past season's hatchlings. On the basis of these data, it is assumed that sexual maturity may be attained by the season following hatching if that occurs in May through August. The

late hatchers (subsequent to August) may not contribute to the breeding population until very late the following season or even the second season following hatching. This problem cannot be resolved without further and more intensive study of growth rates.

Differential growth between males and females is evident. The most apparent difference is a longer axilla-groin length relative to snout-vent length for females (fig. 6). Females also attain a larger snout-vent length than males. In both males and females there is allometric growth of axilla-groin length and length of limbs. The adpressed limbs fail to meet in most males more than 35 mm snout-vent. Three males 41.1 mm, 44.9 mm, and 45.8 mm had overlap of the adpressed limbs. Among the females there were none in excess of 39 mm snout-vent having overlap of adpressed limbs. Similar allometric growth occurs in Mexican forms of this genus (Taylor, 1937).

ACKNOWLEDGEMENTS

I am grateful to Dr. Fred R. Cagle for his help and criticisms during the progress of this study. Drs. E. S. Hathaway, George H. Bick, and George H. Penn also receive my expression of gratitude as do the fellow students who assisted and encouraged me.

I wish to thank Drs. W. D. Stull, C. O. Berg, and W. F. Hahnert, Department of Zoology, Ohio Wesleyan University, for their criticisms of the manuscript.

SUMMARY

1. Four hundred and sixty-two specimens of *Scincella laterale* (Say) were examined to determine size at sexual maturity, seasonal reproductive cycle, and reproductive potential.

2. A series of 32 males and 37 females (Tulane 14108) over 35 mm snout-vent lengths was examined to determine sexual dimorphism in selected characters. Sexual dimorphism is present as regards axilla-groin/snout-vent length, snout-vent/tail length, and dorsal scale row counts, with females having larger axilla-groin/snout-vent length ratio and dorsal scale row counts and males having a larger snout-vent/tail length ratio. No dimorphism exists for mid-body scale row counts or pigmentation.

3. Juveniles were observed to show sexual dimorphism only with respect to dorsal scale row counts as series Tulane 14108 above. Dimorphism with respect to axilla-groin/snout-vent length begins at about 24 mm snout-vent.

4. A positive correlation between axilla-groin and snout-vent lengths exists for both sexes. Males and females differ significantly in this character.

5. Males and females exhibit allometric growth of the axilla-groin length and limb lengths. Adpressed limbs of males less than 35 mm snout-vent and females less that 39 mm snout-vent overlap.

6. The scales on the sides of the neck, base of the tail, in the axilla and groin, and on the posterior surfaces of the limbs are keeled. Occasional individuals may have keels on the dorsal scales as well as the above areas. This is especially true of juveniles. No sexual dimorphism exists as regards these keels.

7. No geographic variation exists for the Louisiana population as regards certain selected morphological characters.

8. Males are sexually mature at 35 mm snout-vent length. Spermatozoa are present in the testes and vas deferens from January through August.

9. Females are sexually mature at a snout-vent length of 35 mm.

10. Ovarian follicles 1 mm or more in diameter are present from December through August. These follicles are assumed to indicate the extent of the breeding season for females. The concurrence of oviducal eggs and follicles of 2 mm or more in diameter is indicative of the possibility of two broods per season. Only females of 44 mm or more in snout-vent length show this potentiality. Oviducal eggs are present from March through August.

11. The average number of oviducal eggs per female is $3.3 \pm .05$, the range from one to five. Eggs were found in the right oviduct only, but not in the left oviduct only. The average number of eggs in the right oviduct, $1.9 \pm .06$, is significantly different from the average of the left oviduct, $1.5 \pm .05$.

12. Hatchlings are those individuals between 16-19 mm snout-vent. Individuals hatched from May to August may reach maturity by the spring following hatching. Late hatched individuals (subsequent to August) may not reach maturity until very late the following season or even until the second season following hatching.

13. Embryos advanced to the somite stage with brain and tail flexures were observed in 30 oviducal eggs from ten females collected in March, June, July, and August.

14. Field studies of egg laying activities, hatching dates, and growth rates are needed to corroborate the assumptions concerning these activities based on laboratory studies.

REFERENCES CITED

ATSATT, S. R. 1953. Storage of sperm in the female chameleon *Microsaura pumila pumila*. *Copeia*, 1953: 59.

BLANCHARD, FRANK N. 1921. A revision of the king snakes: genus *Lampropeltis*. *U. S. Nat. Mus., Bull.* 114: 1-260.

BLOUNT, R. F. 1929. Seasonal cycle of the interstitial cells in the testes of the horned toad (*Phrynosoma solare*). *Jour. Morph. and Physiol.*, 48: 317-343.

BRECKENRIDGE, W. J. 1943. The life history of the blackbanded skink, *Eumeces s. septentrionalis* (Baird). *Amer. Midl. Nat.*, 29: 591-605.

CAGLE, FRED R. 1948a. Sexual maturity in the male turtle, *Pseudemys scripta troostii*. *Copeia*, 1948: 108-111.

1948b. A population of carolina anole. *Chicago Acad. Sci., Nat. Hist. Misc.*, No. 15: 1-5.

CARR, ARCHIE F. 1940. A contribution to the herpetology of Florida. *Univ. Fla. Publ., Biol. Sci. Ser.*, 3: 1-118.

CAZIER, MONT A. and ANNETTE L. BACON. 1949. Introduction to quantitative systematics. *Bull. Amer. Mus. Nat. Hist.*, 93: 349-388.

CIESLAK, EDWIN S. 1945. Relations between reproductive cycle and the pituitary gland in the snake *Thamnophis radix*. *Physiol. Zool.*, 18: 299-329.

COOK, FANNYE, A. 1943. Alligators and lizards of Mississippi. *Surv. Bull., Miss. State Game and Fish Comm.*, pp. 1-20.

DAVIS, WILLIAM B. 1945. The hatchling of *Leiolopisma laterale*. *Copeia*, 1945: 115-116.

KLAUBER, LAWRENCE M. 1937. A statistical study of the rattlesnake. *Occ. Pap., San Diego Soc. Nat. Hist.*, No. 3: 2-56.

1943. Tail-length differences in snakes with notes on sexual dimorphism and the coefficient of divergence. *Bull. Zool. Soc. San Diego*, No. 18: 5-60.

LEWIS, THOMAS HOWARD. 1951. The biology of *Leiolopisma laterale* (Say). *Amer. Midl. Nat.*, 45: 232-240.

MAYR, ERNST. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York, pp. 3-334.

MITTLEMAN, M. B. 1947. American Caudata. I. Geographic variation in *Manculus quadridigitatus*. *Herpetologica*, 3: 209-224.

1950. The generic status of *Scincus lateralis* Say, 1825. *Ibid.*, 6: 17-20.

ORTENBURGER, ARTHUR IRVING. 1928. The whipsnakes and racers, genera *Masticophis* and *Coluber*. *Univ. Mich. Studies, Mem. Univ. Mich. Mus.*, 1: 1-247.

PEATMAN, JOHN GRAY. 1947. *Descriptive and Sampling Statistics*. Harper and Brothers, New York, pp. 3-577.

REYNOLDS, W. E. 1943. The normal seasonal cycle in the male *Eumeces fasciatus* together with some observations on the effects of castration and hormone administration. *Jour. Morph.*, 72: 331-377.

SIMPSON, GEORGE G. and ANNE ROE. 1939. *Quantitative Zoology*. McGraw-Hill Book Company, Inc., New York, pp. 1-414.

Smith, Hobart M. 1946. *Handbook of Lizards of United States and Canada.* Comstock Publishing Company, Ithaca, pp. 1-557.

Snedecor, George W. 1946. *Statistical Methods.* Iowa State College Press, Ames, pp. 1-485.

Taylor, Edward S. 1937. Two new lizards of the genus *Leiolopisma* from Mexico, with comments on another Mexican species. *Copeia,* 1937: 5-11.

Viosca, Percy, Jr. 1933. *Louisiana Out-of-Doors.* Author, New Orleans, pp. 1-187.

Weekes, H. Claire. 1927a. A note on reproductive phenomena in some lizards. *Proc. Linn. Soc. New South Wales,* 52: 25-38.

1927b. Placentation and other phenomena in the scincid lizard *Lygosoma (Hinulia) quoyi. Ibid.,* 52: 499-554

NA- New Orleans

TULANE STUDIES IN ZOOLOGY

Volume 1, Number 3 July 28, 1953

AN OUTLINE FOR THE STUDY OF A REPTILE LIFE HISTORY

FRED R. CAGLE

DEPARTMENT OF ZOOLOGY, THE TULANE UNIVERSITY OF LOUISIANA, NEW ORLEANS.

MUS. COMP. ZOÖL.
LIBRARY
AUG 24 1953
HARVARD
UNIVERSITY

TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

NORMAN HARTWEG, Curator of Amphibians and Reptiles, Museum of Zoology, University of Michigan, Ann Arbor, Michigan.

CHARLES M. BOGERT, Curator, Department of Amphibians and Reptiles, American Museum of Natural History, New York. N. Y.

KARL P. SCHMIDT, Chief Curator of Zoology, Chicago Natural History Museum, Chicago, Illinois.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

Price for this number: $0.75.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University of Louisiana,
New Orleans, U. S. A.

MUS. COMP. ZOOL.
LIBRARY
AUG 24 1953
HARVARD
UNIVERSITY

AN OUTLINE FOR THE STUDY OF A REPTILE LIFE HISTORY

FRED R. CAGLE

Department of Zoology, The Tulane University of Louisiana, New Orleans.

The renewed interest of biologists in natural populations, the development of the new systematics, population genetics, biodemography, and biosociology, i.e. of bionomics, or ecology in the broadest sense, has brought demands for detailed information on life histories of animals. The herpetologist is thus obligated to reexamine many of the standards and customary procedures in natural history. Renewed emphasis is also being placed on the organization of the knowledge comprised in natural history. Investigations in autecology (the ecology of the individual or of the individual species) are aimed toward the development of significant generalizations and principles. The modern systematist should not and must not divorce his thinking from ecology; the ecologist must not ignore systematics. While condemning the ecologist for ignoring systematics, the systematist has often been guilty of ignoring ecology. There is an urgent need for men thoroughly trained in the techniques of both ecology and systematics, men who can accelerate the trend toward a blending of these fields.

The investigator interested in reptilian populations finds but few studies of the bionomics of reptiles that meet critical standards. He finds an assortment of fragmentary facts that are difficult if not impossible to integrate, and often immediately require the test of repetition. It may be pointed out that repetition of field observations in a critical spirit may be fully the equivalent of experimental test. There seems to be a need for a statement of minimum requirements of information basic to the formulation of suggestions for a systematic approach to research on natural populations.

Perhaps the best test of significance of an observation in "natural history" is one similar to the test for the adequate description of a species or subspecies. Does the observation reflect an attribute of a given population? Is it reported in such a fashion that it may be integrated with other observations to state such an attribute? Or, has the research merely reported an aberrant or extreme behavior pattern, an anomalous situation, or such fragmentary data that it fails to express any particular fact as an attribute of a population?

What information is required in a definitive life history investigation? Ideally? What, practically, can the investigator hope to contribute? In what areas of biology may his data be applicable? What are the prevalent fallacies in life history analyses? Some attempt is made here to indicate limits and to designate specifically the obligation of the student interested in natural populations of

reptiles. Many of the techniques developed by the ichthyologist, mammalogist and ornithologist may well be utilized by the herpetologist. There is an urgent need for the development of new techniques of research and for new applications of old ones. The herpetologist does not have the equivalent of the procedure of the ichthyologist for determining the age and growth of an individual by the examination of the growth lines of scales; nor does he have the trapping procedure for systematic sampling as used by the mammalogist, or the activity recording techniques developed by the ornithologist. Equivalents of these techniques are among our greatest needs. All of the needs for herpetological investigation cannot be enumerated in this paper, nor can all of the techniques developed in other fields be mentioned, but the bibliography is intended to provide suggestions and a key to the vast literature.

The herpetologist concerned with the study of a single form cannot hope to explore intensively all of the questions presented in the following discussion, but his awareness of the problems and of the need for information will permit him to make observations that otherwise might not be recorded. A serious report on a life history should be the result of a planned, long term research project. Such a report will integrate all of the minor elements of the topic to be gleaned from the literature with the more directed accumulation of planned observations of the author. The investigator, through proper planning, may maintain several such research programs. The outline that follows is purposely elaborated; and it includes much detail that may appear unnecessary to my colleagues; but it is directed to the students of the future who may be approaching similar problems from both the ecological and the systematic side. An early and comparable effort to systematize studies in life histories that has had a long usefulness is the summary of Walter P. Taylor (1919). Fitch (1949) presents many valuable suggestions for the student interested in natural history.

This paper is the outgrowth of an outline for the study of a reptile life history prepared originally under the direction of Dr. Norman E. Hartweg, University of Michigan. Its development has been encouraged by the critical and generous comments of Mr. Karl P. Schmidt, Chicago Natural History Museum. I am indebted to Mr. Roger Conant, Philadelphia Zoological Garden and Mr. Arthur Loveridge, Harvard University for their suggestions. The group of graduate students in herpetology at Tulane University has been a constant source of stimulating challenge in the preparation of this report. Mr. A. H. Chaney, Mr. Robert Gordon, Mr. Paul Anderson and Mr. Richard Johnson have been of particular aid.

Studies contributing to concepts expressed in this review were aided by a grant from the National Science Foundation.

I. *What are the morphologic characteristics of the population to be studied? Is action taken to insure that the data reported are*

obtained only from individuals of the genus, species or subspecies intended to be studied?

A. What is the taxonomic status of the population? What are the diagnostic features? How are these related to the formal description of the species or subspecies? Are these sharply or only obscurely characterized?

These data are of extreme significance. Excellent information must often be discarded by subsequent workers because the author has failed to indicate clearly the taxonomic characteristics of the population studied. Description must thus be such that any investigator can recognize the population regardless of changes in nomenclature.

B. What other names have been attached to this population?

C. What samples of the population were collected and preserved and where are they deposited? Museum numbers? A representative series supporting the description given must be collected and deposited in a suitable museum collection. Failure to do this is almost characteristic of ecological investigations, yet the conclusion submitted are often not acceptable because of questionable identification of the material on which they are based.

D. What variation is observed in the individuals composing the population? Of what is this variation a reflection? Precise analysis and explanation of individual variation is an obligation. Dice (1952) points out that few museums have adequate storage or curatorial facilities to retain the large number of specimens necessary for the analysis of variation in local populations. The investigator must often utilize materials that cannot be available to future workers; his responsibility is thus multiplied. Through such studies associated with field investigations we may hope to accumulate the data basic to systematic studies at the intraspecies level.

1. What changes in color intensity, in pattern, or morphology occur from birth to old age? Are there any correlated sex differences? How are these changes related to taxonomic investigations? The limited information available on ontogenetic changes in "characters" has resulted in much confusion in taxonomy. The trend in herpetological research toward thorough analysis of such changes promises the development of a basis for substantial clarification of the status of many forms (Oliver, 1951).
2. Is the variation correlated with differences in the external environment?

   With a gradient in the external environment? Is the

the variation due to differences in genotypes or does it reflect the responses of a specific genotype to different environments?

Investigations often query the status of the variation described but do not perform the simplest of experiments aimed at evaluating the genotypic flexibility of the organism studied. Some investigations suggest that some of the characters considered to be of taxonomic importance are merely phenotypic modifications (Fox, 1948). It is essential to the systematist that he determine whether variations are the result of heredity or environment or both.

3. What are the ontogenetic changes in mass as expressed by measurements or weight? What is the maximum size attained? Sex differences?

   Although absolute size is not an acceptable taxonomic character for poikilothermic vertebrates, genetic differences in potential natural longevity or growth potentials may be reflected in differences in maximum sizes between populations (Lagler and Applegate, 1943).

   What procedures were used in mensuration? Weighing?

   Care must be used to insure adequate mensuration practices and to insure that the investigator clearly reports his procedures (Simpson and Roe, 1939; Cazier and Bacon, 1949). Much confusion has been caused by misunderstandings resulting from failure to specify the methods followed. The significance of the limits of error in such data should be borne in mind. When measurements are accurate only to millimeters, proportions calculated to three decimal places give a false aspect of accuracy of the data.

4. What are the principle differential growth changes in each sex? How are these changes related to the major phases of the life history?

   Failure of the systematist to recognize the presence of differential growth has led to the erroneous use of proportions. If detailed quantitative studies cannot be made, the investigator should, as a minimum, designate the gross changes in proportion. This is a particularly acute problem in poikilothermic vertebrates (Hersch, 1941).

II. *What is the geographic range?*

The range should be expressed first in terms of museum specimens or records of authorities. All questionable records

should be deleted. The range definition should indicate the distribution of existing populations (Grobman, 1950). These data may then, in connection with other information, form the basis for the statement of a supposed "true range".

A. What are the factors limiting the range?

These must be considered in terms of the ecological data assembled during the progress of the investigation with particular reference to the total knowledge of the ecological valence of the animal and possible barriers to dispersal (Darlington, 1948; Cowles and Bogert, 1944; Dice, 1952). It is especially important to note that the limiting factors may be entirely different on the different borders of the range of a species (Schmidt, 1950).

B. What physiographic and climatic factors are characteristic of the range?

1. What are the annual temperature and rainfall cycles?
2. What are the mean annual, minimum and maximum temperatures in the warmest and coldest parts of the range?

Whenever feasible, temperature and rainfall data collected by the investigator in the areas of intensive study should be utilized. Of necessity, the investigator must often use meterological and climatological temperatures, but their interpretation should be based on the data of the researcher (Baum, 1950).

3. Does temperature summation (heat summation) affect the distribution of the species investigated?

C. What is the principal habitat? Marginal habitat?

1. Are microclimates of significance? throughout the range? at the periphery of the range? (Geiger, 1950; Diem, 1951).
2. What vegetational types characterize the habitat?
3. Do size or age groups tend to occupy different habitats?
4. Does the animal have an innate habitat recognition mechanism? (Svärdson, 1949; Tinbergen, 1948).

III. *What is the age and sex composition of a local population?*

A. What annual changes occur in the composition of a local population?

1. What is the sex ratio in mature individuals during the breeding season? How does this change during a single year?

Sex ratios are often reported without reference to maturity or to the breeding season although radical changes do occur in some reptile populations. Esti-

mates of the relation of sex ratios to natality should be based only on the relative frequency of mature individuals (Forbes, 1940; Cagle, 1948).

Sex identification is frequently reported without reference to the criteria used. What are these criteria? Secondary sex characters? Gonad condition? If dissection, on what basis was sex determined?

2. What is the sex ratio in juveniles? At birth? In progressive age groups?
3. What annual changes occur in the ratio of juveniles to adults? What is the potential contribution from "young of the year" to the adult segment of the population?
4. Can an ecological life table be constructed?

   The difficulty of determining mortality rates in most reptiles forbids the successful completion of such tables yet an attempt to collect data basic to the estimation of survivorship curves should be made (Deevey, 1947).
5. What are the major predators? Is predation pressure a significant factor in annual and long term cyclic changes? What is the relation of loss from predation to population density? (Errington, 1946).

B. What long-term cyclic changes occur in the composition of the local population? What is the cause of such cycles? Is exhaustion of the adreno-pituitary system a factor as has been demonstrated for some mammal populations? (Christian, 1950; Elton, 1942).

C. Do local populations differ in composition? If so, what is the basis of such differences?

   Adequate local sampling provides a basis for obtaining answers to such questions. It has been demonstrated that substantial differences may be present in the compositions of local populations. Comparison of population samples must be tempered with an awareness of the difficulties of obtaining such samples. Series of specimens preserved in museum collections are rarely unbiased samples of natural populations. The student should note particularly those few long-term studies in local areas (De Haas, 1941).

D. Does the individual animal or the mated pair occupy a home range (or activity range as defined by Carpenter, 1952). Territory?
   1. What is the size of the home range and of the territory?
      a. What features of the habitat may modify the size?

b. What is the relation of the size of the territory or home range to density?

c. Does the individual have homing ability? If so, what are the mechanisms involved in orientation?

The recovery of marked individuals in short-term and long-term studies will provide information on these questions. A wide variety of methods have been used for the marking of reptiles: metal bands or plates (Wickham, 1922); scale clipping (Blanchard and Finster, 1933; Conant, 1948; Fitch, 1949); plate notching (Cagle, 1939); tattooing (Woodbury, 1948); branding (Woodbury and Hardy, 1948); painting (Cagle, 1946). Trapping and other special collecting procedures are described by Dargan and Stickel (1949), Lagler (1943a). The calculation of size of home range from trapping results is discussed by Hayne (1949) and Stickel (1950). Stickel and Cope (1947) summarize information on home ranges. Schaefer (1941), Bailey (1952) and Leslie (1952) discuss the estimation of size of animal populations by marking experiments.

The multiplicity of problems involved in animal orientation are ably discussed by Fraenkel and Gunn (1940).

2. Is the territory selected by the male, female or both? Do both sexes participate in its defense?

a. What are the characteristic behavior patterns used in defense of territory?

Lowe and Norris (1950) summarize the reports of aggressive behavior in snakes.

b. What is the chief stimulus to maintenance of territory?

c. Is the territory maintained throughout the year or or only during short periods?

Nice (1941) presents a classification of the types of territoriality.

IV. *What is the density of the population?*

There should be more than a vague estimate of density expressed as rare, common or abundant. The objective should be to gain a measure of the number of individuals in a given area expressed in terms clearly defined by the investigator. The use of the concepts of abundance, and relative apparent abundance as suggested by Marr (1951) is recommended. The method selected for this determination of abundance

must rest on the knowledge of the ecological requirements of the individual. Kendeigh (1944) provides a suggestive review of the procedures for measurement of bird population. Andrushko (1936) suggests techniques suitable for some species. A summary of methods is presented by Thomas Park (1950). Information of particular value in estimating populations from recovery of marked specimens is given by Ricker (1948), Jackson (1939) and Bailey (1952). This procedure has been applied to reptiles by several authors (Cagle, 1950; Fitch, 1949; Stickel, 1950).

A. What is the relation of density to the questions posed in sections I, D and III A to D (Blair, 1951)?

B. What is the relation of density of the form studied to that of other reptiles inhabiting the area? (Fitch, 1949; Cagle, 1950; Cagle and Chaney, 1950).

V. *What is the potential reproductive capacity? What is the relation to realized reproductive performance? What are the best measures of natality?*

A. At what age and/or size does the animal become sexually mature?

1. When are the secondary sex characters developed? What is the relation of time of their appearance to the potentiality of sexual functioning? (Regamey, 1935)
2. What cyclic changes occur in secondary sex characteristics?
3. What is the relation of age of attainment of maturity to the annual reproductive cycle?

Investigators often fail to indicate what they mean by sexual maturity. Care must be exercised that the criteria for maturity are defined. In reptiles these may concern the presence of oviducal eggs in females, of corpora albicantia, of ovarian follicles of a specified size or ovaries of a specified weight or volume (Altland, 1951). In males a specific stage of spermatogenesis, a specified testicle weight or volume in relation to an indication of total body mass or the presence of motile sperm may be useful (Cieslak, 1945; Cagle, 1944; Risley, 1938; Fox, 1952). No adequate techniques are available for determining the age of an individual reptile. The procedures used by Bryuzgin (1939) should be further explored. Bryuzgin concluded that rings discernible in cleared skull bones of snakes could be used to determine age.

B. What is the total period of reproductive activity in the life of an animal?

1. Does the annual reproductive potential remain the same, decrease or increase with age?
2. When does senility occur?
3. What is the ecological longevity?

C. What is the annual realized reproductive performance?

1. What is the annual period of reproductive activity in females? in males? What is the relation of this period to the total annual activity cycle?

   Baker (1947) discusses the causes of breeding seasons. Volsøe (1944) describes seasonal fluctuations in the reproductive system. Kendeigh (1941) summarizes information on the relation of length of day to gonad development. This period is usually considered as that period in which the females are "carrying" young or are laying eggs. Much confusion has resulted from failure to delimit this period. Thus it may be stated that a female having eggs in the oviduct was collected on a given date. Yet this is not clearly indicative of the time when eggs may be deposited. Each investigator should insure preciseness of definition. Writers frequently use the presence or absence of oviducal eggs to delimit the season but this can lead to potential errors if not weighed properly. Eggs may be retained in the oviducts for long periods (Cagle and Tihen, 1948).

2. What correlation is there between courtship or copulation and ovulation? What is the significance of the sex ratio and population density in relation to annual realized reproductive performance?

   These are little-explored areas in herpetology yet important ones if we are to arrive at an understanding of those factors controlling changes in reptile populations. The fact that some reptile females may bear young or deposit fertile eggs after as long as eight years after copulation suggests that unbalanced sex ratios may be of but scant consequence. The unverified yet not disproven statement that single or successive copulations are essential to stimulate ovulation indicates the importance of a favorable sex ratio. The work of Darling (1938), Vogt (1942), Errington (1946) and others has suggested that population density may markedly affect breeding success.

   a. What is the pattern of courtship?

      Exploration of the courtship patterns with emphasis on interspecies differences promises to yield much of value in explaining the develop-

ment of physiological isolation. Noble and Bradley (1933) furnish many suggestions for procedure and interpretation. Cagle (1950) describes differences in the courtship pattern between two species of the genus *Pseudemys*. Davis (1936) summarizes the literature for snakes; Gloyd (1947) suggests additional problems; Greenberg (1945) summarizes the knowledge of courtship in the family *Iguanidae*.

(1) How does it differ from that of related forms?

(2) What advantages in reproduction are provided by the courtship pattern?

(3) What selective factors function in courtship?

(4) What secondary sex characters are of most significance in courtship?

(5) What senses are involved in courtship? (Noble, 1937)

b. What is the relation of courtship drives to aggregation? (Finneran, 1949).

c. When do ovulation and fertilization occur?

(1) What is the fertilization rate? The relation of successful courtship and copulation to fertilization rate?

(2) Is copulation essential to ovulation? to egg depositions? (Woodward, 1933).

3. How many groups of young (eggs) are produced each year?

This question must usually be answered by the examination of ovaries from chronological samples taken during the breeding season so that progressive changes in number and size of ovarian follicles or total volume or weight may be reported. Too, examinations of the ovaries of females at the end of the reproductive period may yield counts of ovulation points (corpus luteum or corpus albicans) (Samuel, 1952).

4. How many young (eggs) are produced in each group? Some investigators have depended solely upon counts of oviducal eggs or of eggs found in nests. Both procedures are subject to substantial error as the worker can but rarely be confident that no eggs have been previously deposited, that ovluation is completed or that two or more females have not utilized the same nest. Counts of ovulation points are usually more acceptable. Certainly the typical extreme variation in number of eggs and young produced emphasizes that little significance may be attached to many of

the literature reports of the number of young in single females or nests. Counts of young present in the uteri of viviparous or ovoviviparous forms possibly provide the most reliable criteria of clutch size. (The terms, viviparous and ovoviviparous, have been used in varied ways in herpetological literature. It is suggested that the term, ovoviviparous, be restricted to describe a situation in which the developing young gains no sustenance from the female).

a. Is there a correlation between reproductive capacity and size or age? How is this related to estimates of natality in local population?

The large difference in reproductive capacity between small and large females make it exceedingly difficult to utilize much of the published data on reproductive capacity as bases for estimates of natality.

VI. *What are the major factors controlling the relation of the number of surviving young to the number of eggs or young produced by females?*

A. What are the characteristics of the egg at deposition?

1. How do the eggs vary in size, volume and weight in each clutch?

The irregular shape of most reptile eggs reduces the value of measurements of length or width reported without volumes (Lynn and Brand, 1945).

2. Is there any correlation in size and/or weight and size of female?

3. What changes occur in size and weight of eggs during incubation?

The weight and volume of eggs change much and irregularly with age and the environment. Cunningham and Hurwitz (1936) reported that eggs increased as much as 60% in weight during incubation. Data on reptile eggs are of little value unless they are accompanied by statements as to their age and conditions under which they were incubated. The statistical treatment (Edgren, 1949) does not remedy this discrepancy.

4. In what stage of development is the egg at deposition?

a. Does this stage of development vary with the time eggs are retained in the oviducts? If so, how does this influence the incubation period?

b. How is the stage of development related to the egg size and weight?

B. Where and in what manner are eggs deposited?
   1. Is a nest constructed?
      a. What factors determine the nest site?
      b. How is the nest constructed?
      c. What is the relation of choice of nest site and construction to potential survival of young?
      d. What is the behavior pattern of the female constructing a nest? What features are of survival importance?
      e. Does the female use the same nesting site for subsequent clutches? in subsequent years?
   2. Does the female remain with the eggs? return to them? What is the relation of female behavior to survival potential of young? of the females?
      a. Does the female "defend" the eggs?
      b. Does the female contribute "heat" to incubation?

      These questions cannot be answered on the basis of single observations. Behavior of reptiles is sufficiently variable that repeated observations are essential to description of behavior patterns. In most situations the investigator can gain but restricted field data on these questions and is compelled to study captive specimens as a basis for evaluation of field-collected data (Noble and Mason, 1933).

C. What factors determine incubation rates?
   1. What is the period of incubation? in field nests? in the laboratory?
      a. What is the relation of temperature levels or changes to incubation time? of degree-hour to incubation time? (Cunningham, 1939).
      b. Are differences in incubation time between clutches of eggs related to egg-deposition (sequence in oviducts; time of retention in oviducts; quality of shell deposited)? Observers frequently do not state incubation periods in degree-hours and do not provide their criteria for "hatching". The extreme difficulty of evaluating much of the published material makes it unavailable for coherent treatment.

      It is not usually possible to observe the deposition of reptile eggs and the incubation period must be expressed as the interval between the laying of the last egg and the hatching of the last egg. This procedure is usually followed in reporting the incubation time of bird eggs (Skutch, 1950). Although rep-

tiles typically deposit an entire brood over a short period as compared with birds, the total time required to deposit a brood is often significant in relation to the incubation period. The incubation time should be expressed in terms of days and hours or degree-hours.

2. How sensitive are eggs to low or high temperature during the incubation period? What extremes are the eggs subjected to in the typical nest site? Potential mortality?
3. How do the hatchlings escape from the egg? What is the function of the caruncle? What mortality is involved in the process of hatching?

D. Does the female develop any particular behavior traits associated with gestation?

1. What is the period of gestation? (Bragdon, 1951).
2. What are the principle causes of mortality during embryonic development?
3. Does the female tend to select a particular type of site for the birth of the young? Relation of such selection to potential survival?
4. Describe the birth of the young.

VII. *What are the characteristics of the young? Are there any typical behavior traits? What is the relation of the behavior pattern to survival? to growth?*

A. What advantageous resources in morphology, physiology, behavior patterns do the young adults possess? (Daniel and Smith, 1947).

1. What is the amount of yolk retained? Is it utilized as a source of nourishment? How long and under what conditions will it serve to support the young?
2. How long do the young remain in the nest or with the female? What factors influence the length of this period? May young overwinter in the nest? Remain with the female for prolonged periods? What relation may this bear to survival potentialities?

B. What are the major hazards to which the young are exposed immediately after leaving the nest or the female?

VIII. *What are the characteristics of the growth curve of individuals of the local population?*

A. What is the length of the growing season?

1. What are the factors serving to delimit the growing season? Availability of food? Changes in environmental temperature? Cyclic changes independent of temperature?

Various procedures have been attempted for determining the limits of the growing season. The actual observation of initiation and cessation of growth through study of seasonal samples is best but such observations are difficult to obtain. The correlation of formation of growth rings in turtles with season has been attempted (Cagle, 1946). Too, once the minimum and maximum effective temperatures of a form are known they may be utilized to approximate the time of initiation or slowing of activity. This does not, however, necessarily define the growing season as it has been demonstrated that reptiles may become quiescent during the winter although retained at constant temperature. Evans and Hegre (1940) have suggested that some genetic time factor, distinct from the temperature factor, is operative in reptiles.

2. What variations in length of growing season occur within the area of investigation?

   It is indicated by some researches that the time of initiation or cessation of growth may vary significantly from one local habitat or situation to another.

B. What is the annual increment (in that measure selected as the best indicator of total change in mass) during each season of the animal's life? What sex differences occur?

1. What are the factors influencing the rate of growth? (size and/or age; senility, length of growing season, social dominance).
2. What are the limits of variation in growth rates? How does growth rate affect the attainment of maturity, natality, mortality?
3. What age or size groups may be discerned? (Klau and David, 1952).
4. Is growth potentially continuous throughout the life of the individual?

C. What is the natural (ecological) longevity?

1. What longevity records are available from captive sepcimens?
2. What estimates of age may be made from the population samples (Woodbury, 1951).
3. What are the characteristics of youth, maturity, old age?

IX. *What is the annual cycle of activity and what factors exert primary influence on the cycle?* (Fitch and Glading, 1947; Oliver, 1947).

A. What is the relation of the growing season to the period

(periods) of courtship, egg-deposition and birth of young?

B. What are the optimum, minimum and maximum effective body temperatures?

C. What is the seasonal cycle in diel behavior (e.g., in basking) (Girons, 1947).

D. Are the animals quiescent during any period of the year? Are aggregations formed?

1. What preparations are made for the period of quiescence?
2. Where do the animals spend the winter?
3. What environmental factors cause the initiation of quiescence? renewed activity?

   Bailey (1949) demonstrated that the plains gartersnake, *Thamnophis radix* could endure temperatures of approximately —2°C. for a protracted period.
4. What is the composition (age groups, size groups, sex ratios) of the winter aggregation?
5. What is the role of winter quiescence in limiting the geographic distribution? (Bailey, 1948).

X. *What is the diel cycle of activity?*

A. What is the role of basking in the daily cycle?

1. What determines the time of basking, the length of the period?

   Sergeev (1939) reports a close relation between environmental temperature and the period of activity. Benedict (1932) summarizes temperature relations in reptiles.
2. What is the function of basking?
   a. How is the period of basking related to rate of increase or decrease of body temperature?
   b. What is the characteristic behavior pattern in basking. How is this related to control of body temperature? (Cowles and Bogert, 1944; Gunn, 1942; Chernomordikov, 1943; Bogert, 1949).

B. Is feeding restricted to any particular part of the day? How is the feeding behavior or length of the feeding period influenced by food availability?

C. Are breeding activities (courtship; egg-deposition; birth of young) restricted to any part of the day?

D. When does the peak of activity occur in the daily cycle?

E. How is the diel (Klauber, 1939) cycle modified by weather changes, population density?

Interspecies differences in the diel cycle of activity may affect the entire life history. Exploration of the cycle may yield the key to many of the problems presented here. Noble (1946) presents valuable information on such problems.

XI. *What are the food habits? Their relation to growth and survival?*

A. How does the animal obtain its food?

1. Can the animal pursue and catch actively moving prey?
2. What food preferences are exhibited in the field and laboratory?

B. What are the principle foods? Relation to availability?

1. What is the relative importance of the food items?
2. How do feeding habits vary during the life of the animal?
3. Is there any seasonal variation in feeding habits?

Most studies of reptile food habits have reported a high percentage of empty stomachs. It is thus essential that the investigator utilize intestinal as well as stomach contents. Too, the fecal material of many reptiles may be used. Fitch and Twining (1946) emphasize the value of scats in the determination of the food habits of snakes. The scats of lizards, particularly, are of great value in food analysis. Carpenter (1952) obtained data on food habits of snakes by forcing regurgitation. Lagler (1943b) reviews the food habits of Michigan turtles.

C. Does the animal act as a controlling or limiting predator?

XII. *Does this form exhibit any characteristic and genetically limited patterns of group behavior?*

The study of behavior under undisturbed natural conditions often yields startling information of basic importance to the explanation of population problems (Svärdson, 1949; Calhoun, 1950; Carpenter, 1950) and phylogeny (Bellairs and Underwood, 1951). Few zoologists have developed the ability to profit from the observation of field behavior patterns (Emlen, 1950). Herpetologists, particularly have not utilized this procedure.

A. Do aggregations occur? If so what are the stimuli and binding forces in aggregation? the function of the aggregation? (Noble, 1936; Allee, 1931, 1951; Greenberg, 1943.)

B. Are social hierarchies present?

1. If dominance hierarchy is present, what is the relation

to territoriality, natality? (Evans, 1938, 1951; Greenberg, 1943).

2. How does the social hierarchy affect the migrating individual? the juvenile seeking a territory?
3. Does the social hierarchy influence growth and reproductive potential? (Calhoun, 1950).

Such questions as these may be answered if some of the methods of field ornithologists be adapted. The use of blinds and optical equipment for observation will yield much of value to the interpretation of interactions. Observation towers were used to study the behavior of turtles in Illinois (Cagle, 1944; 1950). Excellent suggestions, many of which are of value to the herpetologist, are presented by Emlen (1950). The work of Evans (1938, 1951) is suggestive of problems and procedures.

C. Are there typical defensive or offensive behavior patterns? Bogert (1941) describes the "king-snake defense posture" of rattlesnakes. Mertens (1946) summarizes reports of such actions in reptiles.

LITERATURE CITED

ALLEE, W. C. 1931. *Animal Aggregations. A Study in General Sociology.* Univ. of Chicago Press, Chicago, pp. 1-431.

———— 1951. *Cooperation Among Animals.* Henry Schuman, N. Y. pp. 1-233.

ALTAND, PAUL D. 1951. Observations on the structure of reproductive organs of the box turtle. *Jour. Morph.*, 89: 599-616.

ANDRUSHKO, S. I. 1936. Methods and technique of reptilian censuses in deserts. *Probl. Ecol. Biocenol. Leningrad,* 3: 158-167 (Russian; English summary).

BAILEY, NORMAN T. 1952. Improvements in the interpretation of recapture data. *Jour. Animal Ecol.*, 21: 120-127.

BAILEY, REEVE 1948. Winter mortality in the snake *Storeria dekayi. Copeia,* 1948: 215.

———— 1949. Temperature toleration of gartersnakes in hibernation. *Ecology,* 30: 238-242.

BAKER, JOHN R. 1947. The seasons in a tropical rain-forest (New Hebrides). *Linnean Society's Journal-Zoology,* 41: 248-258.

BAUM, WERNER A. 1950. Ecological use of meteorological temperatures. *Science,* 113: 333-334.

BELLAIRS, A. d'A. and GARTH UNDERWOOD 1951. The origin of snakes. *Biol. Rev.*, 26: 193-237.

BENEDICT, FRANCIS G. 1932. The physiology of large reptiles with special reference to the heat production of snakes, tortoises, lizards and alligators. *Carnegie Inst. Wash.* 425: 1-539.

BLAIR, W. FRANK 1951. Evolutionary significance of geographic variation in population density. *Texas J. Sci.*, 3: 53-57.

BLANCHARD, FRANK N. and ETHEL B. FINSTER 1933. A Method of marking living snakes for future recognition, with a discussion of some problems and results. *Ecology,* 14: 334-347.

BOGERT, CHARLES M. 1941. Sensory cues used by rattlesnakes in their recognition of ophidian enemies. *Ann. N. Y. Acad. Sci.,* 41: 329-344.

---------- 1949. Thermoregulation in reptiles, a factor in evolution. *Evolution,* 3: 195-211.

BRAGDON, DOUGLAS E. 1951. The non-essentiality of the corpora lutea for the maintenance of gestation in certain live-bearing snakes. *Jour. Exper. Zool.,* 118: 419-435.

BRYUZGIN, V. L. 1939. A procedure for investigating age and growth in reptiles. *Comptes Rendus (Doklady) de l'Acad. des Sciences de l' U.S.S.R.,* 23: 403-405.

CAGLE, *Fred* R. 1939. A system of marking turtles for future identification. *Copeia,* 1939: 170-173.

---------- 1944a. Sexual maturity in the female of the turtle *Pseudemys scripta elegans. Copeia,* 1944: 149-152.

---------- 1944b Home range, homing behavior, and migration in turtles. *Misc. Publ. Mus. Zool. Univ. Mich.,* 61: 1-33

---------- 1946. The growth of the slider turtle, *Pseudemys scripta elegans. Amer. Midl. Nat.,* 36: 685-729.

---------- 1948. Sexual maturity in the male turtle *Pseudemys scripta troostii. Copeia,* 1948: 108-111.

---------- 1950. The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). *Ecol. Monogr.,* 20: 31-54.

CAGLE, FRED R. and A. H. CHANEY 1950. Turtle populations in Louisiana. *Amer. Midl. Nat.,* 43: 383-388.

CAGLE, FRED R. and JOSEPH TIHEN 1948. Retention of eggs by the turtle, *Deirochelys reticularia. Copeia,* 1948: 66.

CALHOUN, JOHN B. 1950. The study of wild animals under controlled conditions. *Ann. N. Y. Acad. Sci.,* 51: 1113-1122.

CARPENTER, CHARLES C. 1952. Comparative ecology of the common garter snake *(Thamnophis s. sirtalis),* the ribbon snake *(Thamnophis s. sauritus),* and Butler's garter snake *(Thamnophis butleri)* in mixed populations. *Ecol. Monogr.,* 22: 235-258.

CARPENTER, C. R. 1950. General plans and methodology for field studies of the naturalistic behavior of animals. *Ann. N. Y. Acad. Sci.,* 51: 1006-1008.

CAZIER, MONT A. and ANNETTE L. BACON 1949. Introduction to quantitative systematics. *Bull. Amer. Mus. Nat. Hist.,* 93: 347-388.

CHERNOMORDIKOV, V. V. 1943. On temperature reactions of reptiles. *Zool. J. Moscow,* 22: 274-279.

CHRISTIAN, JOHN J. 1950. The adreno-pituitary system and population cycles in mammals. *Jour. Mamm.,* 31: 247-259.

CIESLAK, EDWIN S. 1945. Relations between the reproductive cycle and the pituitary gland in the snake *Thamnophis radix. Physiol. Zool.,* 18: 299-329.

CONANT, ROGER 1948. Regeneration of clipped subcaudal scales in a pilot black snake. *Chicago Acad. Sci., Nat. Hist. Misc.,* No. 13: 1-2

COWLES, RAYMOND B. and CHARLES M. BOGERT 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Amer. Mus. Nat. Hist.*, 83: 265-296.

CUNNINGHAM, BERT 1939. Effect of temperature upon the developmental rate of the embryo of the diamond back terrapin *(Malaclemys centrata Lat.). Amer. Nat.*, 73: 381-384.

CUNNINGHAM, BERT and A. P. HURWITZ 1936. Water absorption by reptile eggs during incubation. *Amer. Nat.*, 70: 590-595.

DANIEL, ROBERT S. and KARL U. SMITH 1947. The sea-approach behavior of the neonate loggerhead turtle *Jour. Comp. and Physiol. Psych.*, 40: 413-420.

DARGAN, LUCAS M. and WILLIAM H. STICKEL 1949. An experiment with snake trapping. *Copeia*, 1949: 264-268.

DARLING, F. F. 1938. *Bird Flocks and the Breeding Cycle. A Contribution to the Study of Avain Sociability.* Cambridge Univ. Press, Cambridge, England, pp. 1-24.

DARLINGTON, P. J. JR. 1948. The geographical distribution of cold-blooded vertebrates *Quart. Rev. Biol.*, 23: 105-123.

DAVIS, D. DWIGHT 1936. Courtship and mating behavior in snakes. *Zool. Series Field Mus. Nat. Hist.*, 20: 257-290.

DEEVEY, E. S. 1947. Life tables for natural populations of animals. *Quart. Rev. Biol.*, 22: 283-314.

DE HAAS, C. P. J. 1941. Some notes on the biology of snakes and their distribution in two districts of West Java. *Treubia*, 18: 327-375.

DICE, LEE R. 1952. Quantitative and experimental methods in systematic zoology. *Systematic Zool.*, 1: 97-104.

DIEM, M. 1951. Tagesgang der relative Feuchtigkeit in der bodennahen Luftochicht in Gras und über nacktem Humus. *Arch. Meteorol. Geophys. u Bioklimatol., Ser. B*, 2: 441-447.

EDGREN, RICHARD A. 1949. Variation in the size of eggs of the turtles *Cheldydra s. serpentina* (Linne) *Sternotherus odoratus* (Latreille). *Chicago Acad. Sci., Nat. Hist. Misc.*, No. 53: 1.

ELTON, CHARLES 1942. *Voles, Mice and Lemmings. Problems in Population Dynamics.* Oxford, pp. 1-496.

EMLEN, JOHN T. 1950. Techniques for observing bird behavior under natural conditions. *Ann. N. Y. Acad. Sci.*, 51: 1103-1112.

ERRINGTON, P. L. 1946. Predation and vertebrate populations. *Quart. Rev. Biol.* 2: 144-177; 3: 221-245.

EVANS, LLEWELLYN T. 1938. Cuban field studies on territoriality of the lizard, *Anolis sagrei. Jour. Comp. Psych.*, 25: 97-125.

_____ 1951. Field study of the social behavior of the black lizard, *Ctenosaura pectinate. Amer. Mus. Novitates*, No. 1493: 1-26.

EVANS, LLEWELLYN T. and ERLING HEGRE 1940. Endocrine relationships in turtles. *Endocrinology*, 27: 144-148.

FINNERAN, L. C. 1949. A sexual aggregation of the garter snake. *Thamnophis butleri* (Cope). *Copeia*, 1949: 141-144.

FITCH, HENERY S .1945. Notes on social behavior of the collared lizard *Copeia*, 1945: 226-230.

_____ 1949a. Outline for ecological life history studies of reptiles. *Ecology*, 30: 520-532.

---------- 1949b. Study of snake populations in central California, *Amer. Midl. Nat.*, 41: 513-579.

FITCH, HENRY S. and BEN GLADING 1947. A field study of a rattlesnake population. *Calif. Fish and Game*, 33: 103-123.

FITCH, HENRY S. and H. TWINING 1946. Feeding habits of the Pacific rattlesnake. *Copeia*, 1946: 64-71.

FORBES, THOMAS R. 1940. A note on reptilian sex ratios. *Copeia*, 1940: 132.

FOX, WADE 1948. Effect of temperature on development of scutellation in the garter snake. *Thamnophis elegans atratus*. *Copeia*, 1948: 252-262.

---------- 1952. Seasonal variation in the male reproductive system of Pacific Coast garter snakes. *Jour. Morph.* 90: 481-542.

FRAENKEL, GOTTFRIED S. and DONALD L. GUNN 1940. *The Orientation of Animals; Kineses, Taxes, and Compass Reactions*. Oxford, Clarendon Press, pp. 1-352.

GEIGER, RUDOLPH 1950. *The Climate Near the Ground*. Harvard University Press, Cambridge, Mass. pp. 1-482.

GIRONS, H. SAINT 1947. Ecologie des viperes. I *Vipera Aspis*. *Bull. Soc. Zool. France*, 72: 158-169.

GLOYD, HOWARD K. 1947. Notes on the courtship and mating behavior of certain snakes. *Chicago Acad. Sci., Nat. Hist. Misc.*, No. 12: 1-4.

GREENBERG, BERNARD 1943. Social behavior of the western banded gecko, *Coleonyx variegatus* Baird. *Physiol. Zool.*, 16: 110-122.

GROBMAN, ARNOLD B. 1950. The problem of the natural range of a species. *Copeia*, 1950: 231-232.

GUNN, D. L. 1942. Body temperatures in poikilothermal animals. *Biol. Rev.*, 14: 293-313.

HAYNE, DON W. 1949. Calculation of size of home range. *Jour. Mamm.* 30: 1-18.

HERSH, A. H. 1941. Allometric growth; the ontogenetic and phylogenetic significance of differential rates of growth. *3rd Growth Symposium*: 113-145.

JACKSON, C. H. N. 1939. The analysis of an animal population. *Jour. Anim. Ecol.*, 8: 238-246.

KENDEIGH, S. C. 1941. Length of day and energy requirements for gonad development and egg-laying in birds. *Ecology*, 22: 237-248.

---------- 1944. Measurement of bird populations. *Ecol. Monogr.*, 12: 67-106.

KLAU, HELENE H. and PAUL R. DAVID 1952. The bimodality of length distribution in *Heterodon p. platyrhinos L.* and its relation to the season in which the specimens were collected. *Amer. Midl. Nat.*, 47: 364-371.

KLAUBER, L. M. 1939. Studies of reptile life in the arid southwest. *Bull. Zool. Soc. San Diego*, 14: 1-100.

LAGLER, KARL F. 1943a. Methods of collecting freshwater turtles. *Copeia*, 1943: 21-25.

---------- 1943b. Food habits and economic relations of the turtles of Michigan with special reference to fish management. *Amer. Midl. Nat.*, 29: 257-312.

LAGLER, KARL F. and VERNON C. APPLEGATE 1943. Relationship between the length and the weight in the snapping turtle. *Chelydra serpentina* Linnaeus. *Amer. Nat.*, 77: 476-478.

LESLIE, P. H. 1952. Ehe estimation of population parameters from data obtained by means of the capture-recapture methods. II. The estimation of total numbers. *Biometrika*, 49: 363-388.

LOWE, CHARLES H. JR. and KENNETH S. NORRIS 1950. Aggressive behavior in male sidewinders. *Crotalus cerastes*, with a discussion of aggressive behavior and territoriality in snakes. *Chicago Acad. Sci., Nat. Hist. Misc.* No. 66: 1-13.

LYNN, W. GARDNER and THEODOR VON BRAND 1945. Studies on the oxygen consumption and water metabolism of turtle embryos. *Biol. Bull.*, 88: 112-125.

MARR, JOHN C. 1951. On the use of the terms abundance, availability and apparent abundance in fishery biology. *Copeia*, 1951: 163-169.

MERTENS, ROBERT 1946. Die Warn-und Droh-Reaktionen der Reptilien. *Abk. Senck. Naturf. Ges.*, 471: 1-108.

NICE, MARGARET 1941. The role of territory in bird life. *Amer. Midl. Nat.*, 26: 441-487.

NOBLE, RUTH CROSBY 1946. *The Nature of the Beast.* Doubleday and Co., Inc., pp. 1-224.

NOBLE, G. K. 1936. The aggregation behavior of *Storeria dekayi* and other snakes, with special reference to the sense organs involved. *Ecol. Monogr.*, 6: 269-316.

_____ 1937. The sense organs involved in the courtship of *Storeria, Thamnophis* and other snakes. *Bull. Amer. Mus. Nat. Hist.*, 73: 673-725.

NOBLE, G. K. and H. T. BRADLEY 1933. The mating behavior of lizards: its bearing on the theory of sexual selection. *Ann. N. Y. Acad. Sci.*, 35: 25-100.

NOBLE, G. K. and E. R. MASON 1933. Experiments on the brooding habits of the lizards *Eumeces* and *Ophisaurus*. *Amer. Mus. Nov.*, No. 619: 1-29.

OLIVER, JAMES A. 1947. The seasonal incidence of snakes. *Amer. Mus. Novitates*, No. 1363: 1-14.

_____ 1951. Ontogentic changes in osteodermal ornamentation in skinks. *Copeia*, 1951: 127-130.

PARK, THOMAS 1950. Chapter 18. General properties of populations. IN: *Principles of Animal Ecology*, pp. 263-271.

REGAMEY, JEAN 1935. Les caractères sexuels du Lézard *(Lacerta agilis L.) Revue Suisse de Zoologie*, 42: 87-168.

RICKER, WILLIAM E. 1948. Methods of estimating vital statistics of fish populations. *Indiana Univ. Publ., Sci. Series*, 15: 1-101.

RISLEY, P. L. 1938. Seasonal changes in the testis of the musk turtle, *Sternotherus odoratus* L. *Jour. Morph.*, 63: 301-317.

SAMUEL, MARY 1952. Histogenesis and development of the corpus luteum in *Cerberus rhyncops* (Schneider). *Jour. Zool. Soc. India*, 3: 201-310.

SCHAEFER, MILNER B. 1951. Estimation of animal populations by marking experiments. *Fishery Bull.* U. S. Fish andWildlife Service, 52 (69): 191-203.

SCHMIDT, KARL P. 1950. The concept of geographic range with illustrations from amphibians and reptiles. *Texas Jour. Sci.*, 2: 326-334.

SERGEEV, A. 1939. The body temperature of reptiles in natural surroundings. *Comptes Rendus (Doklady) de l'Acad. des Sci. de l'USSR*, 22: 49-52. (Russian).

SIMPSON, GEORGE GAYLORD and ANNE ROE 1939. *Quantitative Zoology*. McGraw-Hill Book Co., pp. 1-414.

SKUTCH, ALEXANDER F. 1950. Outline for an ecological life history of a bird, based upon the song tanager, *Ramphocelus paserinii costaricensis*. *Ecology*, 31: 464-469.

STICKEL, LUCILLE 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). *Ecol. Monogr.*, 20: 351-378.

STICKEL, WILLIAM H. and JAMES B. COPE 1947. The home ranges and wanderings of snakes. *Copeia*, 1947: 127-236.

SVÄRDSON, GUNNAR 1949. Competition and habitat selection in birds. *Oikos*, 1: 157-174.

TAYLOR, WALTER P. 1919. Suggestions for field studies of mammalian life-histories. *U. S. Dept. Agric., Circ.* No. 59: 1-8.

TINBERGEN, N. 1948. Social releasers and the experimental method required for their study. *Wilson Bull.*, 60: 6-51.

VOGT, WILLIAM 1941. A practical lizard trap. *Copeia*, 1941: 115.

_____ 1942. Informe sobre las Aves guaneras elevado a la Compania Administradora del Guano. *Bol. Comp. Admin. Guano*, 18: 3-132.

VOLSØE, H. 1944. Structure and seasonal variation of the male reproductive organs of *Vipera berus* (L.). *Spolia Zoologica Musei. Haunienses Copenhagen*, 5: 7-172.

WICKHAM, M. M. 1922. Notes on the migration of *Macrochelys lacertina*. *Proc. Okla. Acad. Sci.*, 2: 20-22.

WOODBURY, ANGUS M. 1948. Marking reptiles with an electric tattooing outfit. *Copeia*, 1948: 127-128.

_____ 1951. Introduction—A ten-year study. A snake den in Tooele County, Utah. *Herpetologica*, 7: 4-14.

WOODBURY ANGUS M. and ROSS HARDY 1948. Studies of the desert tortoise. *Gopherus agassizii*. *Ecol. Monogr.*, 18: 145-200.

WOODWARD, S. J. 1933. A few notes on the persistence of active spermatozoa in the African night-adder, *Causus rhombeatus*. *Proc. Zool. Soc. London*, 1933: 189-190.

NA-New Orleans

TULANE STUDIES IN ZOOLOGY

Volume 1, Number 4 August 15, 1953

A POPULATION OF HOLBROOK'S SALAMANDER, *EURYCEA LONGICAUDA GUTTOLINEATA* (HOLBROOK).

ROBERT E. GORDON

DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY OF LOUISIANA, NEW ORLEANS

MUS. COMP. ZOÖL.
LIBRARY

AUG 24 1953

HARVARD
UNIVERSITY

TULANE UNIVERSITY

NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

COLEMAN J. GOIN, Associate Professor of Biology, University of Florida, Gainesville, Florida.

CLIFFORD H. POPE, Curator, Division of Reptiles and Amphibians, Chicago Natural History Museum, Chicago, Illinois.

FRED R. CAGLE, Professor of Zoology, Tulane University of Louisiana, New Orleans.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

Price for this number $0.25.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University of Louisiana,
New Orleans, U. S. A.

AUG 24 1953
HARVARD
UNIVERSITY

A POPULATION OF HOLBROOK'S SALAMANDER, *EURYCEA LONGICAUDA GUTTOLINEATA* (HOLBROOK).

ROBERT E. GORDON
Department of Zoology, Tulane University of Louisiana, New Orleans.

Knowledge of the life cycle and general ecology of many of the more abundant North American caudate amphibians is variously incomplete or lacking. Holbrook's salamander, *Eurycea longicauda guttolineata* is no exception. The literature records of this form are based on a few recently metamorphosed individuals or larvae. No samples have been available from which information relative to variation and population structure can be obtained. Two samples, collected from the same population in 1950 and 1952, are deposited in the collections of Tulane University (Tulane 13314 and 14905).

The author is indebted to Allan H. Chaney for information concerning the 1950 sample, collected by the 1950 Tulane Field Crew, and to Mr. Chaney and Robert G. Webb for aid in securing the 1952 sample. Both collections were taken during field trips made possible by grants for summer research to Dr. Fred R. Cagle, to whom the author owes much for opportunity to participate in the 1952 field expedition and for valued criticism of this manuscript.

Both samples were taken approximately two miles south of Marianna, Jackson Co., Florida on the Chipola River, the same locality mentioned by Chaney and Smith (1950) and Tinkle (1952), although the latter was misinformed as to the distance from Marianna. Sixty-three individuals (Tulane 14905), collected in three man hours, were taken on August 23, 1952 between 2:30 and 3:30 P.M. The salamanders were collected in an irregularly shaped depression, approximately three-quarters of an acre in size, located in the river's floodplain. Piles of debris and high water marks indicated previous inundation, although no surface water was present. The vegetation was predominately gum-cypress, with ironwood occupying the drier edges of the area. The understory was sparse. A thick grass-herb layer was encroaching toward the center from the drier sides of the depression. The habitat fits Carr's (1940) description of the "Low Hammock." Fallen timber and other surface litter was abundant.

The majority of the salamanders was collected from patches of ground devoid of vegetation, but dense in surface debris and cypress knees. Individuals were found under all sizes of debris; as many as three were found under the same cover. The sky was overcast and rain imminent. Several of the salamanders were active and could be seen moving on the surface.

Associated species found under surface debris with *Eurycea l. guttolineata* were *Desmognathus fuscus fuscus, Microhyla carolinensis, Eumeces fasciatus,* and *Diadophis punctatus punctatus.*

The second sample, collected July 12, 1950, consists of eighty-one specimens, approximately half of which (according to information supplied by A. H. Chaney) were found in the area of the 1952 sample by Chaney. The other individuals were taken in adjacent areas along the river.

Gonadal Development and Egg Deposition

The gonads of 144 individuals were examined macroscopically. The gonads and accessary ducts of 56 specimens in the size range (snout-vent) 21 to 39 mm (mean 34) are distinctly immature. The testes and ducts contain no pigment. The compact ovaries contain many small white ovocytes not enlarged with yolk material.

Eighty-eight specimens (varying in size from 43 to 61 mm, mean 52 mm) possess enlarged gonads and ducts when compared to the above group. The testes and vasa deferentia are pigmented in varying degrees. The ovocytes appear to contain yolk material.

Forty-seven females (40 in the 1950 sample and 7 in the 1952 sample) constitute a size group falling within the range 46 to 61 mm, average 53 mm. A correlation between condition of the oviduct, ovary and body length is apparent (fig. 1). Twenty-four individuals in the size range 46 to 54 mm (mean 50) possess compact ovaries containing ovocytes of approximately the same size. The oviducts are firm, flat and without convolution (fig. 1, open squares).

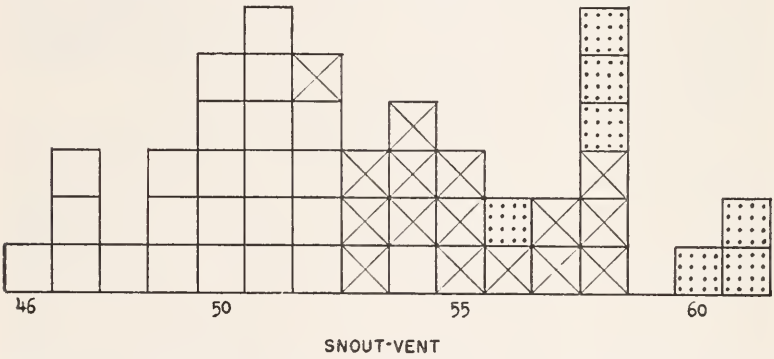


Figure 1. Ovarian condition correlated with body length. Each square represents one individual. Open squares indicate ovaries compact, oviducts straight. Squares with diagonals, ovaries contain luteal-like structures and oviducts convoluted. Dotted squares indicate compact ovaries and convoluted oviducts, and represent specimens taken in August. All other individuals were collected in July.

Twenty-three individuals in the size range 53 to 61 mm (average 56) possess one feature in common, the oviduct is always convoluted (at least one loop is present) and, in the majority of individuals, this convolution occurs in the proximal end. The ovaries of the July 1950 individuals (squares with diagonals, fig. 1) vary in the number of collapsed follicles present. These same structures have been referred to as "corpora lutea" by McCurdy (1931), and presumably are the remains of former ovarian follicles after ovulation has occurred (McCurdy, *op. cit.;* Fisher and Richards 1950). Three individuals with snout-vent lengths of 54, 58 and 56 mm possess no collapsed follicles. The ovocytes are of two distinct sizes and the oviducts are convoluted. All of the females collected in August 1952 (dotted squares, fig. 1) possess ovaries which have completely recovered, *i.e.* no collapsed follicles are present, ovocytes are of two distinct sizes,

but the oviducts are convoluted.

The possession of a convoluted oviduct, at least prior to the egg-laying season, seems to indicate that the individual has ovulated at least once. This feature, plus the varying degrees of recovery from ovulation, permits us to divide the sample into two groups, those individuals which have ovulated and presumably are sexually mature, and a group which is becoming sexually mature and will be ready for ovulation during the next reproductive season.

This interpretation is in sharp contrast with that made by Pope and Pope (1949) for *Plethodon glutinosus glutinosus.* They report a group of twelve "spent" individuals (collected in late June, late July and the first week in August) having ovaries which were not compact, the eggs being of various sizes, and whose oviducts were not swollen or convoluted. The body lengths of these individuals are shorter than (yet overlap those of) a series of eleven obviously gravid specimens (Pope and Pope, *op. cit.,* fig. 63). The reproductive season is extended, presumably from June, or late May, through September (Pope and Pope, *op. cit.*).

The testis and vas deferens do not lend themselves as nicely to macroscopic examination as do the female structures. Francis (1934) reports that the Mullerian and Wolffian ducts are never pigmented in female *Salamandra* while ". . . Muller's duct, and its associated urino-genital duct . . ." are always pigmented in the male. Goin (1950) states that the sex of *Ambystoma c. bishopi* may be determined ". . . by examination of the Mullerian duct, which is pigmented in the males and unpigmented in the females . . .". Pigmentation appears macroscopically to be confined to that portion of the vas deferens (urino-genital or Wolffian duct) from which Muller's duct is indistinguishable macroscopically (Francis, *op. cit.*) in mature male *Eurycea.* Twenty-five males in the size range 43 to 54 mm (average 50) possess vasa deferentia of which less than 50 percent of the surface area is pigmented (see fig. 2). Of these, eight individuals (average 50, extremes 48 to 54 mm) have no pigmentation, or melanophores are faintly noticeable bilaterally along a line near the dorsal surface of the duct. The duct in all of the twenty-five males is firm and straight, exhibiting no convolutions. Sixteen specimens, ranging from 51 to 58 mm, mean 54, have vasa deferentia which are convoluted but vary from complete to partial pigmentation, always exceeding 50 percent of the surface of the duct. In this latter group, pigmentation is absent from the proximal part of the duct, the distal part being pigmented and convoluted. From the study of all individuals, the spread of pigmentation seems to be from the distal to the proximal end of the duct.

A general increase of pigmentation with size is suggested; this may possibly be correlated with age and sexual maturity. If it is correlated with the latter, then, as in the females, we have two groups of animals, one (diagonal squares, fig. 2) sexually mature, having been sexually active in one reproductive season; the other group (open squares, fig. 2) just becoming sexually mature, will be ready for sexual activity during the next reproductive season.

Sexual maturity is apparently reached at the same size in both sexes.

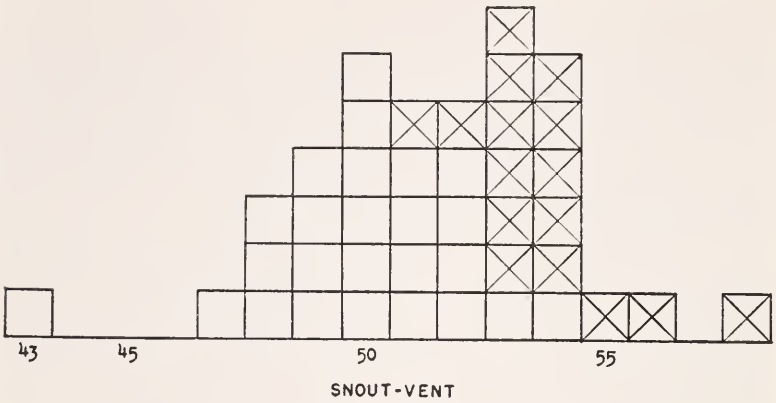


Figure 2. Condition of vasa deferentia correlated with body length. Open squares indicate vas deferens pigmented less than 50 percent, no convolutions. Squares with diagonals, vas deferens pigmented 50 percent or more and convoluted. Each square represents one individual.

All evidence in the literature points to egg deposition in December since females collected in November contain large ovarian eggs (Brimley 1896, 1939; Parker 1948). Females collected in August 1952 possess ovocytes of two distinct sizes and represent the largest individuals in the August sample. The largest females collected in the July 1950 sample show varying degrees of recovery from the "spent" ovarian condition. It would appear that egg deposition occurs in late autumn for this Florida population, possibly in December. It is interesting to note the length of the recovery phase from ovulation until maturing ovocytes again make up the bulk of the ovary.

Vomerine Teeth

Counts were made on 144 individuals. Since only 39 percent of the specimens have the same number of teeth on both sides, the sum of the right and left counts is used in all calculations (see Pope and Pope, 1949). Two individuals were discarded since the vomerine teeth were not clearly separable from those of the parasphenoid. There is no significant difference between the sexes in the number of vomerine teeth. An increase in number of teeth with size is indicated. Males less than 40 mm (snout-vent) have an average of 14.4 teeth, while females of a similar size group possess averagely 14.2 teeth. Of the individuals measuring more than 40 mm, males average 19.8 teeth and females 19.7 teeth.

Body Measurements

The means and extremes for the various body measurements are presented in Table 1. All measurements are in millimeters. Snout-vent length is measured from tip of the snout to the anterior edge of the vent. Head length is measured from the tip of the snout to the gular fold. Head width is a measurement taken across the head at the angle of the jaws. The axilla-groin measurement is the distance between the limb insertions.

Table 1. Body measurements.

No.	Snout-vent	Axilla-groin	Head length	Head width
		Sexually mature		
♂	51.4	28.1	11.5	8.5
41	43 - 58	23 - 32	7 - 13	7 - 9
♀	52.9	29.6	11.6	8.0
47	46 - 61	24 - 35	10 - 14	7 - 9
		Sexually immature		
♂	34.2	18.3	8.3	5.7
33	29 - 37	16 - 20	7 - 9	5 - 6
♀	34.6	18.6	8.5	5.8
22	31 - 39	16 - 21	8 - 9	5 - 7

The mature female reaches a total length only slightly larger than the male. The average length for thirty-nine females is 148 mm (extremes 122 to 167 mm). Thirty-four mature males average 147 mm in total length (extremes 125 to 165 mm).

Population Structure

Sex ratio.—The sex ratios do not deviate significantly from an expected 1 to 1 ratio of either the 1950 sample taken as a unit, the 1952 sample, or the two distinct size groups represented by both samples combined.

Table 2. Sex ratios.

Sex	1950	1952	Juvenile	Adult
♂	40	34	33	41
♀	40	29	22	47

Size groups.—The July 1950 sample (open squares, fig. 3) is composed (with a single exception) of individuals in the size group 43 to 58 mm (snout-vent). These specimens as indicated above are either sexually mature or would presumably have been mature by the December 1950 reproductive season.

Parker (1948) reports that larvae collected in April measure 31 to 34 mm total length. Bishop (1943) gives the measurements of larvae collected June 18 as varying from 22 to 39 mm. The measurements of two recently transformed individuals are reported by Sinclair (1951) as 22.5 and 24 mm body length, and 41.5 and 45 mm total length. The single juvenile in the July 1950 sample measures 21 and 45 mm for the two lengths, and probably represents a recently metamorphosed individual.

The body length frequency of the August 1952 sample presents a distinctly different picture (squares with diagonals, fig. 3). Only eight individuals are sexually mature. Fifty-five specimens (average 34, extremes 29 to 39 mm) are sexually immature and apparently represent individuals metamorphosing the previous June or July.

If we assume that sexual maturity is reached in the second reproductive season following metamorphosis, *i.e.* when the salamander is two years old, then the unusual distribution of size groups in the two samples may be explained in the following way.

It may be postulated that the collection of a large segment of adults in July 1950, by reducing egg deposition the following December, would reduce the number of sexually maturing individuals in 1952. This would explain the absence of the size group 42 to 55

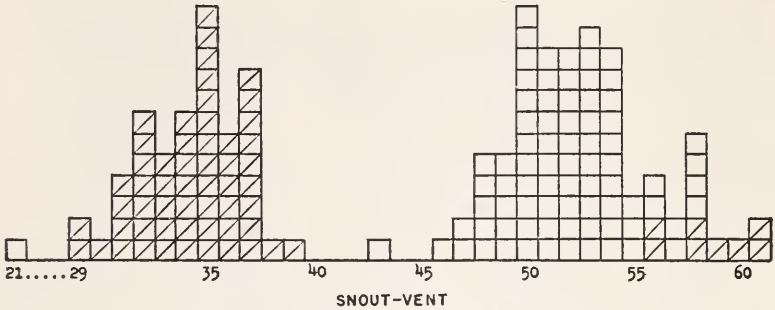


Figure 3. Frequency distribution—snout-vent length. Open squares indicate specimens collected July 1950. Squares with diagonals indicate specimens collected August 1952. Each square represents one individual.

mm in August 1952. The adults which reproduce in 1951 are products of the eggs of 1949. Since the 1950 collection did not interfere with deposition of eggs in 1949, nor with the newly metamorphosed individuals from these eggs, adults would be present to reproduce in December 1951. Egg deposition occurred and the larvae transformed in June or July. The August 1952 sample reveals a preponderance of this group of metamorphosed individuals.

No obvious explanation is available for the absence of a larger segment of the adults which bred in December 1951 from the August 1952 sample; however, differential habitat selection is known to occur in many terrestrial salamanders and may be a possible explanation in this instance.

References Cited

Bishop, Sherman C. 1943. *Handbook of Salamanders.* Comstock Publishing Company, Ithaca, pp. 1-555.

Brimley, C. S. 1896. Batrachia found at Raleigh, N. C. *Amer. Nat.*, 30: 500-501.

---------- 1939. The amphibians and reptiles of North Carolina. *Carolina Tips* [Elon College, N. C.], 2: 18.

Carr, Archie F., Jr. 1940. A contribution to the herpetology of Florida. *Univ. Fla. Stud., Biol. Sci. Ser.*, 3: 1-118.

Chaney, Allan H. and Clarence L. Smith. 1950. Method for collecting mapturtles. *Copeia*, 1950: 323-324.

Fisher, Helen T. and A. Richards. 1950. The annual ovarian cycle of *Acris crepitans* Baird. In *Researches on the Amphibia of Oklahoma*, Univ. Okla. Press, Norman, pp. 129-142.

Francis, Eric B. T. 1934. *The Anatomy of the Salamander.* The Claredon Press, Oxford, pp. 1-381.

Goin, Coleman J. 1950. A study of the salamander, *Ambystoma cingulatum*, with the description of a new subspecies. *Ann. Carg. Mus.*, 31: 299-320.

McCurdy, Harriet M. 1931. Development of the sex organs in *Triturus torosus*. *Amer. Jour. Anat.*, 47: 367-403.

Parker, Malcolm V. 1948. A contribution to the herpetology of western Tennessee. *Jour. Tenn. Acad. Sci.*, 12: 20-30.

Pope, Clifford H. and Sarah H. Pope. 1949. Notes on the growth and reproduction of the slimy salamander, *Plethodon glutinosus*. *Fieldiana*, 31: 251-261.

Sinclair, Ralph M. 1951. Notes on recently transformed larvae of the salamander *Eurycea longicauda guttolineata*. *Herpetol.*, 7: 68.

Tinkle, Donald W. 1952. Notes on the salamander, *Eurycea longicauda guttolineata*, in Florida. *Field and Lab.*, 20: 105-108.

NA-N[ew Orleans]

TULANE STUDIES IN ZOOLOGY

Volume 1, Number 5 September 1, 1953

A REDESCRIPTION OF THE CRAWFISH *PROCAMBARUS HINEI* (ORTMANN) (DECAPODA, ASTACIDAE).

GEORGE HENRY PENN,
DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY OF LOUISIANA, NEW ORLEANS.

MUS. COMP. ZOOL. LIBRARY
SEP 4 1953
HARVARD UNIVERSITY

TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

HORTON H. HOBBS, JR., Associate Professor of Biology, Univer- of Virginia, Charlottesville, Virginia.
FENNER A. CHACE, JR., Curator, Division of Marine Invertebrates, United States National Museum, Washington, D. C.
WALDO L. SCHMITT, Head Curator, Department of Zoology, United States National Museum, Washington, D. C.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

When citing this series authors are requested to use the following abbreviations: *Tulane Stud. Zool.*
Price for this number: $0.25.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University of Louisiana,
New Orleans, U. S. A.

A REDESCRIPTION OF THE CRAWFISH *PROCAMBARUS HINEI* (ORTMANN)

(Decapoda, Astacidae).

GEORGE HENRY PENN,
Department of Zoology, Tulane University of Louisiana, New Orleans.

MUS. COMP. LIBRARY
SEP 4 19
HARVARD UNIVERSITY

The crawfish which is the subject of this paper was named in honor of the late James Stewart Hine (1866-1930), a distinguished student of the Diptera, who was a summer visitor at the now non-existent Gulf Biologic Station, Cameron, Louisiana. Dr. Hine sent the type specimens to Dr. Arnold E. Ortmann at the Carnegie Museum who described the species in 1905. Until recently this species was known only from Cameron as recorded by Ortmann (1905), Cary (1906) and Cary and Spaulding (1909); the latter two references are merely repetitions of Ortmann's original data. In 1939 under a grant from the New Orleans Academy of Sciences I collected crawfishes in southern Louisiana and found this species in several additional parishes. Later, Hobbs (1945) recorded it from Liberty County, Texas as a co-inhabitant at the type locality of *Cambarellus puer* Hobbs. The distribution and ecology of *Procambarus hinei* will be discussed at length in a subsequent paper on the Louisiana species of the genus *Procambarus*.

Ortmann's original description was inadequate and the figure of the first pleopod of the form I male left much to be desired. Specimens used in drawing up the following redescription were collected in two areas in Cameron Parish, Louisiana, each within fifteen miles of the type locality.

PROCAMBARUS HINEI (ORTMANN)

Synonymy.—*Cambarus (Cambarus) hinei* Ortmann, 1905, Ohio Nat., 6: 401; *Procambarus hinei* (Ortmann), Hobbs, 1942, Amer. Midl. Nat., 28: 342.

Type locality.—"One quarter mile from Gulf Beach, near Cameron, Cameron Parish, Louisiana"; type unknown (or lost). The types are not in the Carnegie Museum along with the rest of Ortmann's material (Brooks, 1931), nor have they been located in the crawfish collections of any other institution.

Male, form I.—Cephalothorax (figs. 1, 2) subovate. Abdomen narrower than and slightly longer than the cephalothorax. Width of cephalothorax at widest point subequal to height at the same point.

Areola broad, about 3½ times longer than width at its narrowest point (average, 3.47; range, 3.78 to 2.86), with about five very fine punctations in narrowest part (average, 5.5; range, 5 to 7). Cephalic portion of cephalothorax about 2¼ times as long as the areola (average, 2.26; range 2.15 to 2.44); length of areola averages 30.6 percent of the total length of the cephalothorax (range, 29.0 to 31.7 percent).

Rostrum without lateral spines, but with margins interrupted in most specimens; less than ten percent of the specimens with very small lateral spines on rostrum. Rostrum widest at base, margins raised, more or less straight and converging; no median carina. Acumen distinct, although its base merges with the remainder of the rostrum.

Postorbital ridges weakly developed, terminating anteriorly in small spines. Branchiostegal spine small, acute. Cervical groove interrupted by a very small lateral spine on each side. In some specimens this spine is absent. Epistome (fig. 3) broader than long, with a small spine on anterior margin.

Cephalic region of the telson with two spines in each caudolateral angle, the more lateral one nearly twice the length of the other.

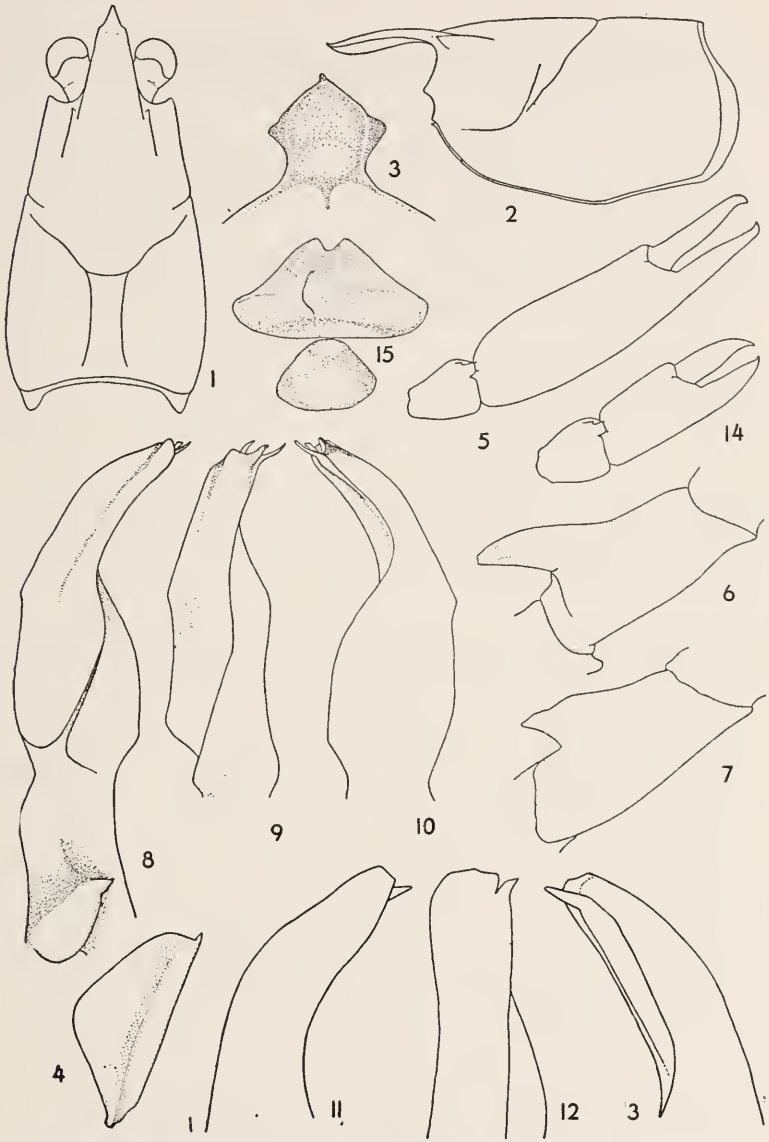
Antennules of usual form, with a large spine on the distal margin of the ventral surface of the basal segment. Antenna reaching just beyond the telson. Antennal scale (fig. 4) extending well beyond the tip of the rostrum; lateral margin straight, terminating in an acute spine; lamellar portion flat, fringed with long hairs from base to apex; greatest width of scale just proximal to the middle, length about 2¼ times greatest width (average, 2.23; range, 2.00 to 2.50).

Chela (fig. 5) subcylindrical, long and slender; non-tuberculate; very finely pubescent; palm inflated. Both fingers terminating in short corneous tips bent toward each other. Opposable margins of fingers flattened and covered with about four (apical) to about ten (basal) rows of small rounded tubercles. Fingers very short; dactyl about 35 percent of the total length of the outer margin of the chela (average, 35.2; range, 32.0 to 37.0). Carpus (fig. 5) subcylindrical, non-tuberculate.

Hooks (figs. 6, 7) on ischiopodite of third and fourth pereiopods; those of the fourth about two-thirds as long as those on third pereiopods.

Venter of cephalothorax covered with a dense mat of long hairs which are present on the mesial faces of all of the pereiopods and maxillipeds. They are especially thick and conspicuous on the mesial faces of the third maxillipeds and the first three pereiopods.

First pleopod (figs. 8, 9, 10) extending to caudal side of the coxopodite of the third pereiopods when the abdomen is flexed. Apical third of pleopod bent caudad at about a 60° angle to the shaft. Pleopod terminating in three very small parts. The apical elements are somewhat twisted counterclockwise so that the mesial and cephalic processes are shifted to a more posterior position than is normal; hence, they are most clearly seen when the caudal surface of the pleopod is examined. Mesial process non-corneous, spiculiform and extending laterodistad; cephalic process corneous, lying near to and mesiocaudad of the mesial process, truncate near apex, and extending laterodistad; central projection corneous, acute and somewhat compressed along its longitudinal axis, with fusion line of



Figures 1 - 15. *Procambarus hinei* (Ortmann): **1, 2,** cephalothorax of form I male; **3,** epistome of form I male; **4,** antennal scale of form I male; **5,** chela and carpus of form I male; **6, 7,** hooks on ischiopodites of third and fourth pereiopods of form I male; **8, 9, 10,** mesial, caudal and lateral views of the first pleopod of form I male; **11, 12, 13,** mesial, caudal and lateral views of the first pleopod of form II male; **14,** chela and carpus of female; **15,** annulus ventralis of female. Pubescence removed from all structures illustrated.

its component elements clearly visible. Caudal process not developed. A shoulder-like hump is present on the cephalomesial part of the apex of the pleopod. Apical half of mesial surface of pleopod with a heavy clothing of long hairs.

Male, form II.—Very similar to form I in general appearance. Chelae reduced but with the ratio of length of fingers to length of chela as in the form I male. Hooks on ischiopodites of third and fourth pereiopods greatly reduced. Venter of cephalothorax only sparsely clothed with long hairs. First pair of pleopods (figs. 11, 12, 13) reaching to posterior part of coxopodites of third pereiopods when abdomen is flexed; apical processes reduced and non-corneous.

Female.—Similar to form I male in shape and structure of the cephalothorax, but differing strikingly in the proportions of the chelae (fig. 14) in which the palm is only slightly longer than the fingers. Annulus ventralis (fig. 15) immovable, roughly pyramidal in shape with the apex of the base directed anteriorly; width nearly twice as great as length. Anterior face with a deep furrow from the base to the summit of the pyramid along the anterior edge. Sinus originates at the summit of this furrow and runs posterodextrad and gently curves back posterosinistrad nearly to the base of the posterior face of the pyramid.

Measurements.—Following are measurements in millimeters for the largest and smallest of the form I males, and the largest female in the collections examined.

	♂ I (largest)	♂ I (smallest)	♀ (largest)
Cephalothorax:			
Length	20.0	14.5	22.0
Height (greatest)	9.9	7.1	11.0
Width (greatest)	9.8	7.6	11.0
Areola:			
Length	6.0	4.3	7.5
Width (narrowest)	1.7	1.5	2.0
Rostrum:			
Length	5.5	4.5	5.6
Width at base	3.1	2.2	4.2
Antennal scale:			
Length (lateral margin)	5.2	4.3	5.5
Width (greatest)	2.5	1.9	2.7
Abdomen:			
Length (to tip of telson)	27.0	18.5	27.0
Chela:			
Length of outer margin	18.0	10.5	9.0
Length of inner margin of palm	11.5	5.8	3.8
Width of palm (greatest)	4.5	2.4	3.5
Thickness of palm (greatest)	3.5	2.0	2.4
Length of dactyl	5.9	3.9	4.5

Color pattern.—Although all of my specimens are faded so that the exact color cannot be recognized, the following notes made some

years ago will at least indicate the color pattern. Dorsally with a pair of conspicuous dark, broad, parallel, longitudinal stripes which originate just below the postorbital ridges and run posteriorly along either side of the areola and onto the abdomen. On the abdomen these stripes converge slightly, become narrower and terminate on the base of the telson. At their termination the stripes are about half as wide as at their points of origin. The sides of the abdominal tergites each have a thin longitudinal, darker stripe. Chelae without dark markings.

Specimens examined.—The specimens used in this study were collected from two localities in Cameron Parish, Louisiana as follows:

5 ♂♂$_{I}$, 8 ♂♂ juveniles, 3 ♀♀, and 7 ♀♀ juveniles, from a shallow pond on the coastal chenier at Creole, April 22, 1940, P. Viosca, Jr. and G. H. Penn (TU P-553). Included in the same collection were a few each of *Procambarus blandingii acutus* (Girard) and *P. clarkii* (Girard).

32 ♂♂$_{I}$, 9 ♂♂$_{II}$, and 14 ♂♂ juveniles, from a shallow pond at Hackberry, July 28, 1940, G. H. Penn (TU P-557). Included in the same collection were a few each of *Cambarellus puer* Hobbs and *Procambarus clarkii* (Girard).

Relationships.—Ortmann (1905: 403) placed *P. hinei* in the *Blandingii* Section on the basis of the hooks on its third and fourth pereiopods and the subcylindrical chelae, and in the *Alleni* Group because of the shape of its rostrum and width of its areola. He did state, however, that "within the latter group it stands rather isolated with regard to the male organs, which show a rather primitive conformation, with exception of the distinct backward curve of the distal part." However, Hobbs (1942: 70-71) pointed out that *P. alleni* (Faxon) itself is a very disjunct species, and he thus considers the *Alleni* group to be monotypic and probably belonging in the *Barbatus* Section. In view of the peculiarities of the structure of the first pleopod of the form I male, *Procambarus hinei* cannot be placed in the same group with *P. alleni,* nor even in the same section; neither can it be placed logically in any of the other sections of the genus as currently described. Accordingly, I am designating a separate section, the *Hinei* Section, to accommodate this disjunct species.

REFERENCES CITED

Brooks, Stanley T. 1931. List of types of Crustacea in the collection of the Carnegie Museum on January 1, 1931. *Ann. Carnegie Mus.*, 20: 161-167.

Cary, L. R. 1906. A contribution to the fauna of the coast of Louisiana. *Gulf Biologic Sta., Bull. No.* 6: 50-59.

Cary, L. R. and H. M. Spaulding 1909. Further contributions to the marine fauna of the Louisiana coast. *Gulf Biologic Sta., Bull. No.* 12: 3-21.

Hobbs, Horton H., Jr. 1942. The crayfishes of Florida. *Univ. Fla. Publ, Biol. Sci. Ser.*, 3(2): 1-179.

---------- 1945. Two new species of crayfishes of the genus *Cambarellus* from the Gulf coastal states, with a key to the species of the genus. *Amer. Midl. Nat.*, 34: 466-474.

ORTMANN, A. E. 1905. A new species of *Cambarus* from Louisiana. *Ohio Nat.*, 6: 401-403.

PENN, GEORGE H. 1941. Preliminary report of a survey of the crawfishes of Louisiana. [Abstract] *New Orleans Acad. Sci., Abstr. Pap. 88th Ann. Meet.*, 1941: 8.

MA New Orleans

TULANE STUDIES IN ZOOLOGY

Volume 1, Number 6 September 15, 1953

A NEW BURROWING CRAWFISH OF THE GENUS *PROCAMBARUS* FROM LOUISIANA AND MISSISSIPPI

(DECAPODA, ASTACIDAE)

GEORGE HENRY PENN,

DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY OF LOUISIANA, NEW ORLEANS.

MUS. COMP. ZOOL. LIBRARY

SEP 18 1953

HARVARD UNIVERSITY

TULANE UNIVERSITY

NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

HORTON H. HOBBS, JR., Associate Professor of Biology, University of Virginia, Charlottesville, Virginia

FENNER A. CHACE, JR., Curator, Division of Marine Invertebrates, United States National Museum, Washington, D. C.

WALDO L. SCHMITT, Head Curator, Department of Zoology, United States National Museum, Washington, D C.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

When citing this series authors are requested to use the following abbreviations: *Tulane Stud. Zool.*

Price for this number: $0.25.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University of Louisiana,
New Orleans, U. S. A.

LIBRARY
SEP 18 1953
HARVARD
UNIVERSITY

A NEW BURROWING CRAWFISH OF THE GENUS *PROCAMBARUS* FROM LOUISIANA AND MISSISSIPPI

(DECAPODA, ASTACIDAE)

GEORGE HENRY PENN,
Department of Zoology, Tulane University of Louisiana, New Orleans.

The new species of *Procambarus* described herein occurs over a fairly wide geographic area, however, it has never been found in large numbers and is a rarely encountered form. Ecologically it may be included among the secondary burrowers (Hobbs, 1942: 20). The relationships of this new species are not clear and will be discussed following the description.

PROCAMBARUS PLANIROSTRIS, *sp. nov.*

Holotype male, form I.—Body subovate, appearing somewhat compressed; abdomen about equal to length of cephalothorax (29.0 - 27.5 mm). Height of cephalothorax (figs. 1, 2) slightly less than width in region of caudodorsal margin of the cervical groove (12.5 - 13.0 mm); greatest width of cephalothorax slightly caudad of caudodorsal margin of the cervical groove.

Areola narrow (20 times longer than width), with a single punctation in the narrowest part; cephalic portion of cephalothorax about 1.75 times as long as the areola; length of areola about 36 percent of total length of cephalothorax.

Rostrum without lateral spines; widest at base, margins slightly raised and only slightly thickened, converging at acumen. Upper surface almost flat, moderately punctate. Acumen small, directed dorsally at tip.

Postorbital ridges reduced, terminating anteriorly without spines; lateral surface excavate. Branchiostegal spine small. Cervical groove interrupted laterally; lateral spine reduced to the size of a large tubercle. Lateral surfaces of cephalothorax granulate, dorsal surface moderately granulate.

Cephalic region of telson with spines in each caudolateral angle, three on right, five on left.

Epistome (fig. 3) slightly more than twice as wide as long, with slightly concave center; cephalic margin with a small spine.

Antennae nearly equal to total length of the crawfish; of normal form. Antennal scale (fig. 4) narrow; widest a little distad of middle; lateral margin inflated, straight and terminating distally in a small spine; total length less than length of areola (8.5 - 10.0 mm).

Chela (fig. 5) with palm inflated; fingers slightly depressed; setiferous punctations present over dorsal surface of most of palm and both fingers. Inner margin of palm with a row of eight prominent

tubercles. Both fingers terminating in short corneous tips, that of the dactyl overhanging the other when the fingers are closed. Thirteen rounded tubercles at base and one distally-located corneous tubercle on opposable margin of immovable finger; fourteen rounded tubercles in corresponding positions on the dactyl. Upper surface of dactyl with seven strong tubercles basally.

Carpus (fig. 5) with five strong spines on distal end in a semicircular arrangement extending medioventrally from dorsal to ventral condyles which articulate with the chela. Upper surface with smaller tubercles toward inner margin and scattered setiferous punctations generally.

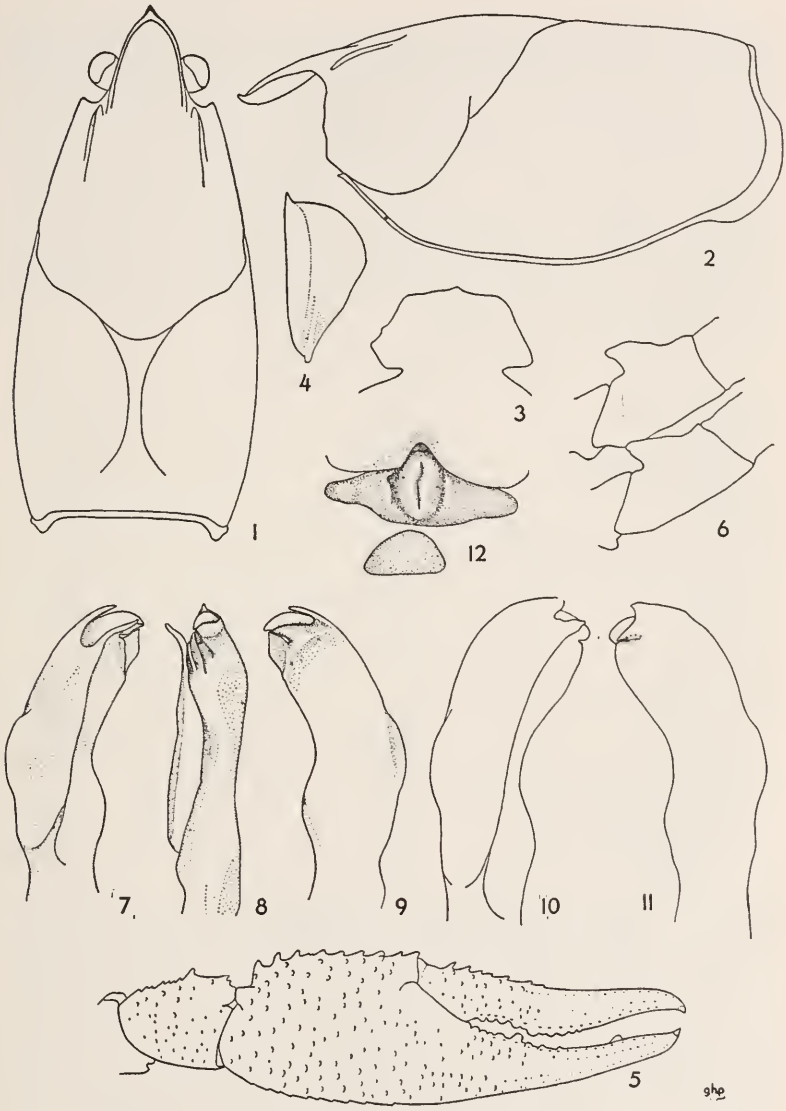
Simple hooks (fig 6) present on ischiopodites of third and fourth pereiopods; length of each greater than half the diameter of the respective ischiopodites.

First pleopod (figs. 7, 8, 9) reaching to anterior side of the coxopodite of the third pereiopods when the abdomen is flexed. Apex terminating in four distinct parts which as a unit extend cuadad at about a 40° angle to the shaft of the pleopod. Mesial process noncorneous, spiniform, directed caudodistad, and not extending beyond the other terminal parts; cephalic process corneous, arising on mesial side of the central projection, directed caudodistad, excavate on caudolateral surface, and closely applied to the central projection; central projection corneous, compressed, "beak-like" in shape, with apex directed caudad; fusion line of centrocaudal and centrocephalic components clearly indicated. Caudal process consisting of two corneous parts: mesially a low, longitudinal ridge flanked laterally by a leaflike element which extends distally, its apex coming in contact with the overhanging central projection. Cephalic margin of the shaft of the pleopod with a distinct shoulder.

Morphotype male, form II.—Very similar to holotype in general appearance; chelae and hooks on ischiopodite of the third and fourth pereiopods greatly reduced. First pair of pleopods (figs. 10, 11) reaching to middle of coxopodites of third pereiopods when the abdomen is flexed; all processes reduced and non-corneous.

Allotype female.—Very similar to holotype in general appearance; chelae greatly reduced. Annulus ventralis (fig. 12) immovable, roughly spindle-shaped with center produced into a cone-shaped protuberance on either side of which is a shallow groove. The sinus originates on the center line a short distance removed from the anterior margin then proceeds through a gently zigzag course to the apex of the central, cone-shaped protuberance. The sternum of the preceding thoracic segment is slightly produced so that its posterior margin underhangs the anterior margin of the annulus.

Color.—The following color notes were made from living mature specimens collected at the type locality. In general this is a drab-colored species. The effect is that of a light tan overcast with olive



Figures 1 - 12. *Procambarus planirostris*, sp. nov.: **1, 2,** cephalothorax of the holotype; **3,** epistome of the holotype; **4,** antennal scale of the holotype; **5,** chela and carpus of the holotype; **6,** hooks on ischiopodites of the third and fourth pereiopods of the holotype; **7, 8, 9,** mesial, caudal and lateral views of the first pleopod of the holotype; **10, 11,** mesial and lateral views of the morphotype; **12,** annulus ventralis of the allotype. Pubescence removed from all structures illustrated.

dorsally on the cephalothorax; the rostrum tan only. Abdomen dorsally with an inconspicuous wide stripe of olive-tan which tapers to a point on the base of the telson; background color of abdomen on either side of the dorsal stripe is a light tan with very fine flecks of darker reddish-tan; this background color extends also onto the dorsal surface of the telson and uropods. On the dorsolateral parts of the abdominal tergites there is a row of spots of olive, one on the anterior margin of each tergite, and connected longitudinally by a faint line of olive. Chelae of the same basic color as the background color of the abdomen, but tubercles capped with black or dark brown, giving the chela and carpus a fine-spotted appearance. One specimen had a faint bluish cast to the fingers.

Measurements.—As follows, in millimeters:

	Holotype	Allotype	Morphotype
Cephalothorax:			
Length	27.5	20.0	29.0
Width (greatest)	13.5	10.0	14.0
Height (greatest)	12.5	9.5	13.5
Areola:			
Length	10.0	7.5	10.5
Width (at narrowest point)	0.5	0.5	0.7
Rostrum:			
Length	5.5	4.0	6.5
Width at base	5.5	3.5	5.5
Abdomen:			
Length (to tip of telson)	29.0	22.0	29.0
Right chela:			
Length of outer margin of hand	25.5	11.0	21.0
Length of dactyl	15.0	6.0	12.0
Width of palm (greatest)	8.5	4.0	7.5
Thickness of palm (greatest)	6.0	2.5	5.0
Length of inner margin of palm	10.0	4.0	8.0

Type locality.—The holotype and allotype were collected from a low area of mixed hardwood, pine and palmetto flatwoods one mile south of Walker (on Louisiana highway 336), Livingston Parish, Louisiana. The holotype was taken on February 17, 1951 by Dr. R. D. Suttkus when the area was inundated by about a foot of water; the allotype was collected on August 29, 1952 by the author and C. E. Biggs from a simple burrow with a neat chimney, around the base of which there was about six inches of standing water. The soil here is a whitish clay and the burrow extended to about twelve inches beneath the soil surface. At the same place there were numerous burrows of *Cambarus hedgpethi* Hobbs and *Orconectes clypeatus* (Hay).

The morphotype was collected from a small creek three miles south of Janice, Perry County, Mississippi on January 28, 1951 by Dr. Fred R. Cagle. No other crawfishes were found at this locality.

Disposition of types.—The holotype, allotype and morphotype are deposited in the United States National Museum, catalogue numbers 95674, 95675, and 95676 respectively. The paratypes are in the following collections: Academy of Natural Sciences, Philadelphia (1 ♂I, 2 ♂♂ juv., and 1 ♀), the personal collection of Dr. Horton H. Hobbs Jr. at the University of Virginia (1 ♂I, 1 ♂ juv., and 1 ♀), and Tulane University (2 ♂♂I, 7 ♂♂ juv., 4 ♀♀, and 6 ♀♀ juv.).

Geographic distribution.—The type series of *Procambarus planirostris* was collected from the "Florida" parishes of southeastern Louisiana and southern Mississippi. These records and a summary of the deposition of these specimens are as follows. LOUISIANA: *East Baton Rouge Parish:* 9 mi. s. Baton Rouge, January 26, 1949, G. H. Bick and L. L. Ellis (TU 910); *Livingston Parish:* 1 mi. s. Walker, February 17, 1951, R. D. Suttkus (USNM, TU 2278), same locality, July 19, 1952, G. H. Penn, R. D. Suttkus and C. E. Biggs (ANS, HHH), same locality, August 20, 1952, G. H. Penn and C. E. Biggs (USNM); *St. Tammany Parish:* Lake Pontchartrain at Mandeville, February 22, 1935, P. Viosca, Jr. and H. B. Chase (TU P-610); *Washington Parish:* 6 mi. nw. Enon, August 10, 1948, G. H. Penn and M. H. Penn (ANS), Franklinton, March 27, 1949, F. R. Cagle (ANS, HHH), 2 mi. n. Varnado, March 3, 1953, F. R. Cagle (TU 2894). MISSISSIPPI: *Perry County:* 3 mi. s. Janice, January 28, 1951, F. R. Cagle (USNM, TU 2853).

Relationships.—*Procambarus planirostris* appears not to belong definitely in any of the sections of *Procambarus* as currently recognized, but has certain characteristics of each of two sections, and apparently occupies a somewhat intermediate position between the two. It shows affinities with the *Barbatus* Section (Hobbs, 1942: 35-36) in its general body conformation and in that the cephalic process of the first pleopod arises from the mesial side of the central projection, but differs from members of this section in lacking the accessory cephalodistal ridge or knob-like prominence. It shows closer affinities with the *Clarkii* Subgroup of the *Blandingii* Section as defined by Hobbs (1942: 93, 98-99) in possessing a distinct shoulder on the cephalic margin of the first pleopod, and in the general configuration of the annulus ventralis.

Because *P. planirostris* exhibits this peculiar combination of characteristics a new section to accommodate it could be justified. However, because of its assumed closer relationship to the species of the *Clarkii* Subgroup of the *Blandingii* Section than to those of the *Barbatus* Section, I am placing it in a separate subgroup, the *Planirostris* Subgroup in the *Blandingii* Section. This action necessitates the modification of Hobbs' diagnosis (1942: 93) with regard to the cephalic process of the first pleopod to the following: cephalic process when present arises from cephalic or cephalolateral margin in all species except those of the *Planirostris* Subgroup in which it arises from the mesial side of the central projection.

REFERENCE CITED

HOBBS, HORTON H., JR. 1942. The crayfishes of Florida. *Univ. Fla. Publ., Biol. Sci. Ser.*, 3(2): 1-179.

TULANE STUDIES IN ZOOLOGY

Volume 1, Number 7 October 23, 1953

THE LIFE HISTORY OF THE CRAWFISH *ORCONECTES (FAXONELLA) CLYPEATUS* (HAY)

(DECAPODA, ASTACIDAE)

ELSIE WAYNE SMITH,

DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY, NEW ORLEANS.

MUS. COMP. ZOOL. LIBRARY

OCT 27 1953

HARVARD UNIVERSITY

TULANE UNIVERSITY

NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico and the Caribbean Sea. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

HORTON H. HOBBS, JR., Associate Professor of Biology, University of Virginia, Charlottesville, Virginia.

THOMAS PARK, Professor of Zoology, University of Chicago, Chicago, Illinois.

GEORGE H. PENN, Associate Professor of Zoology, Tulane University, New Orleans, Louisiana.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

When citing this series authors are requested to use the following abbreviations: *Tulane Stud. Zool.*

Price for this number: $0.50.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University,
New Orleans, U. S. A.

MUS. COMP. ZO
LIBRARY
OCT 27 19
HARVARD
UNIVERSITY

THE LIFE HISTORY OF THE CRAWFISH *ORCONECTES (FAXONELLA) CLYPEATUS* (HAY)

(Decapoda, Astacidae)

ELSIE WAYNE SMITH,[1]
Department of Zoology, Tulane University, New Orleans.

The details of the life histories of comparatively few species of crawfishes in the United States have been studied, however the life history of at least one species in each of the four major genera is fairly well known. Within the genus *Orconectes* two species of the subgenus *Orconectes* have been well studied: *O. propinquus propinquus* (Girard) by Creaser (1933a) in Michigan, and by Van Deventer (1937) and Bovbjerg (1952) in Illinois; and *O. immunis immunis* (Hagen) by Tack (1941) in New York. The subject of the present study, *O. clypeatus,* a member of the subgenus *Faxonella,* has a somewhat distinctive life cycle which might prove to be characteristic of this subgenus alone.

When this study was begun practically nothing had been published concerning either the ecology or life cycle of the species. The entire literature may be summarized in a few sentences. Hay (1899) described it as *Cambarus clypeatus* on the basis of a single female collected from a skiff at Bay St. Louis, Hancock County, Mississippi. From the date of this inauspicious first scientific recognition, *clypeatus* remained a species of questionable affinities (*c.f.* Faxon, 1914) until Creaser (1933b) described the first and second-form males and redescribed the female from two series of specimens collected in Louisiana and Alabama. He also included brief notes describing the "pools along the roadside" and "pools in a bog or swamp" respectively in which it was collected and included the statement that "many burrows were found along the edge of these pools . . . no doubt this species is a burrower, for the pools certainly dry at certain seasons of the year." Later the same year, Creaser and Ortenburger (1933) recorded *O. clypeatus* from Oklahoma and repeated Creaser's notes on its ecology. Lyle (1938) recorded it from Mississippi without comment. Hobbs (1942) recorded it from Florida, Georgia, Alabama and Arkansas and described its burrows along the sides of a roadside ditch in Jackson County, Florida as "marked by small, neatly constructed chimneys, simple, and ranging in depth from six inches to a foot." Penn (1942) recorded the species as abundant in a "pine barren pond" in Louisiana. Finally, Penn (1952) published a compilation of the data of the distribution and ecology of the species in Louisiana.

Within the boundaries of Louisiana *O. clypeatus* is one of the commonest species of crawfishes, and occurs in the following variety of habitats as listed by Penn (1952); temporary situations (58%), including roadside ditches, pineland sloughs, puddles and borrow pits, potholes in dry creek beds, and burrows; permanent situations (42%),

[1] Present address: Savannah, Georgia.

including ponds, creeks, rivers, swamps and swamp ponds. Within the state it occupies these habitats in all physiographic regions except the recent alluvial lands and coastal marshes. The overall distribution of the species as presently known includes the Coastal Plain from southeastern Oklahoma to northeastern Arkansas and Georgia.

THE STUDY AREA

The life history of *O. clypeatus* was studied from October 1949 through January 1951 by means of field observations and statistical analyses of periodic samples of a natural population. The population which was studied and from which the samples were collected was located in a pineland ditch 2.4 miles south of Hickory, St. Tammany Parish, Louisiana. The ditch itself lay to the south side of an unused logging road which formed a retaining levee for an extensive, permanently inundated slough on its north side. The ditch was about 200 feet long, from one to two-and-one-half feet deep, and from three to five feet wide. On the bottom and along the sides, the ditch was covered with a thick carpet of *Juncus repens* Michx. throughout the entire year, and at least some parts of the ditch were shaded throughout each day.

Drought conditions, characterized by the complete absence of standing water anywhere in the ditch, and wet conditions characterized by the presence of standing water throughout the ditch, both occurred periodically during the study period (Table 1). During the wet periods the water level fluctuated with the amount of local rainfall, occasionally overflowing the banks. Usually either one or the other situation obtained when sampling was done, but an intermediate condition existed in which the deeper parts of the ditch were wet and the shallower parts dry. At such times separate samples were collected from each situation. Other crawfishes present in the ditch were numerous *Cambarellus shufeldtii* (Faxon) and occasional *Procambarus blandingii acutus* (Girard).

METHODS OF STUDY

The primary approach to the study was the analysis of periodic samples removed from the population. Collections of samples were originally planned for four week intervals over a period of sixteen months, but it was not practical to adhere strictly to this schedule. A total of sixteen samples on fourteen dates was collected; however, samples for six of the sixteen months are not represented (Table 1). During November and December 1949, drought conditions prevailed and, although field trips were made, the burrowing population was not found. During the other four months, January, March, August and November 1950, no field trips were made because of transportation difficulties.

The samples were collected by dipnet during the wet periods and by digging during the dry periods. Both methods were used along the sides of and in the middle of the ditch for each collection. From one-fourth to one-third of the length of the ditch was sampled when the ditch was wet, but during drought conditions the slower and more

TABLE 1.

BASIC DATA FOR HICKORY, LA. SAMPLES OF *Orconectes clypeatus*.

Lot Number	Date of Collection	Condition of Ditch	Type of Sample		Maximum Water Depth (in inches)	Number (and percentages) of Specimens in Sample			Total
			Water	Burrows		♂ I	♂ II	♀	
	1949:								
1583	Oct. 16	Wet	X		15	3 (4.4)	48 (70.5)	17 (25.1)	68
——	Nov. 25	Dry		X	0	0	0	0	0
——	Dec. 6	Dry		X	0	0	0	0	0
	1950:								
1799	Feb. 24	Wet	X		12	28 (3.6)	343 (44.2)	405 (52.2)	776
1885	Apr. 9	Wet	X		10	46 (10.2)	194 (42.8)	213 (47.8)	453
1946	May 12	Intermediate		X	6	5 (2.7)	102 (53.1)	85 (44.2)	192
1972	June 2	Dry		X	0	4 (2.9)	83 (60.6)	50 (36.5)	137
1980	June 13	Wet	X		12	16 (4.9)	158 (47.9)	156 (47.2)	330
2017	July 12	Dry		X	0	5 (8.5)	22 (37.3)	32 (54.2)	59
2022	July 15	Intermediate	X		3	37 (22.0)	58 (34.5)	7 (43.5)	168
2207	Sep. 29	Intermediate	X		6	88 (67.1)	7 (5.4)	36 (27.5)	131
2208	"	"		X	6	1	1	2	4
2218	Oct. 16	Dry		X	0	0	3	1	4
2229	Oct. 27	Dry		X	0	13 (86.6)	1 (6.7)	1 (6.7)	15
2246	Dec. 1	Dry		X	0	1 (7.0)	2 (10.7)	14 (82.3)	17
2255	Dec. 29	Wet	X		12	7 (1.7)	163 (47.3)	177 (51.0)	347
	1951:								
2261	Jan. 24	Wet	X		12	18 (1.9)	422 (44.2)	515 (53.9)	955

laborious digging was restricted to from one-sixteenth to one-eighth of the length of the ditch.

The first sample made from burrows was taken in the second dry period (May 1950) after the study was begun. The burrows were found over the bottom and along the sides of the ditch and each was marked only by an inconspicuous entrance hole, usually less than three-fourths of an inch in diameter; chimneys were never seen. Below the entrance each burrow branched off into several tunnels, which eventually led to individual pockets or "cells" from eight to fifteen inches beneath the surface. Each pocket was occupied by one crawfish only.

Although this collection established the fact that the population burrowed during dry periods, the possibility that a portion of it might migrate during such times remained to be determined. Accordingly, each time a visit was made to Hickory, the slough across the road was checked with a dipnet for a migrating part of the population. Only six individuals of *O. clypeatus* were found in the slough and these only during wet periods following times when the ditch could have overflowed and flooded the road. If drought is a necessary factor for the completion of the life cycle of this species then the facts that the road was seldom flooded and that the unpopulated slough always contained water explains the scarcity of this species in collections from the slough. It was felt therefore that the absence of *O. clypeatus* from collections during the October-November 1949 drought was a result of faulty technic in sampling, not of an absence of the burrowing population.

The majority of the samples was preserved in alcohol either in the field or immediately upon return to the laboratory. Some first-form males, collected December 1, 1950, and some ovigerous females, collected between September and December 1950, were kept alive for observation in the laboratory.

In the laboratory the length of the cephalothorax was measured on all specimens. This measurement was taken on an observed mid-dorsal line from the tip of the rostrum to the end of the cephalothorax. All measurements were made with an ocular micrometer calibrated for a stereoscopic microscope. Each measurement was estimated to the nearest part of a micrometer unit but was converted for recording only to the nearest one-tenth (0.1) of a millimeter. As it was measured and recorded each specimen was assigned a sub-lot number and kept in an individual vial until the entire lot (*i.e.*, sample) had been completely studied.

A series of females was selected for the study of ovarian egg growth and production. After an ovary had been removed, the eggs were teased from it in a dish of water. Eggs were measured along their longest diameters and recorded to the nearest hundredth of a millimeter (0.01). Total ovarian egg count was recorded for only a few of the females so analysed.

A few specimens, in addition to certain samples, were collected separately and kept alive for observation in the laboratory. Such in-

dividuals were placed each in separate bowls or small aquaria containing rain water, sand, and usually some vegetation. All were fed Pablum.

STATISTICAL ANALYSES

A detailed discussion of the statistical analyses used in this study is not included in this paper. However, since the conclusions and interpretations of the life cycle are based largely on statistical methods, a brief summary of the methods employed and the steps of the various analyses is included here.

Methods used in the statistical analyses were modeled closely on those given by Peatman (1947) and Cazier and Bacon (1949). The measurement of cephalothorax length was taken as the criterion of age, but sexual maturity was based on other well-established biological criteria, *i.e.,* attainment of first form in the males, and maturation of ovarian eggs or the ovigerous condition in the females.

Since it was anticipated that each sample would give a clue to the stage of development of the entire population during a given time fragment in its annual cycle, it was necessary first to determine the homogeneity or extent of heterogeneity of the apparent age components (*i.e.,* size groups) of each sample. This was done following the grouping of measurements according to the following criteria: (1) each sample was kept separate according to time and place (*i.e.,* either aquatic or burrowing); (2) females, first-form males, second-form males, and unsexed young were separated into sub-groups respectively whenever they occurred in any one sample. At this point the sub-groups of the samples were each considered to be homogeneous on the fundamentals of location, time, and sex, but not on age.

Determination of homogeneity of age of these groups was based on three hypotheses: (1) that the frequency distribution of the cephalothorax length describes the form of the normal curve when the group is homogeneous; (2) that those groups which do not fit the normal curve, do not because of the presence of more than one age group within the group tested, and vice versa, those groups that do, do so because of the presence of only one age group; and, (3) that the heterogeneous groups (according to age only) can be resolved into their homogeneous components under certain conditions.

Grouped data were used throughout the study for all calculations of mean, standard deviation, and for those other statistics that were based upon the mean or standard deviation. The criteria for class groupings of the samples were: one-tenth millimeter (the very youngest crawfishes); two-tenths millimeter (the maturing groups), and five-tenths millimeter (the adult groups).

The first hypothesis was proved by using a set of young crawfish removed from the pleopods of their mother, thus of a known uniform (or homogeneous) age (Table 2, Dec. 1, group "j"). The second and third hypotheses, dependent on the proof of the first, were resolved by applying the chi-square Test of Significance to the separate frequency distributions of each of the sub-groups already known to be homogeneous except for age. The results (chi-square probabilities)

TABLE 2.

BASIC STATISTICS FOR GROUPS OF FEMALES AND UNSEXED JUVENILES

Date	Group	Number of Specimens	Cephalothorax Length in Millimeters		P
			Actual Range	Mean	
1949:					
Oct. 16	Q	1	18.8	—	—
	R	16	13.4 — 16.1	14.9	.50
1950:					
Feb. 24	a	5	5.2 — 5.8	—*	—*
	A	333	6.0 — 10.0	8.0	.02
	I	17	10.3 — 12.7	11.0	.50
	S	46	13.8 — 18.6	15.7	.99
Apr. 9	b	6	7.8 — 8.8	—	—
	B	141	8.9 — 12.3	10.6	.30
	II	39	13.0 — 16.9	15.1	.50
	T	30	15.5 — 18.2	16.7	.50
	W	3	19.0 — 19.6	—	—
May 12	c	1	8.1	—	—
	C	80	9.8 — 13.3	11.5	.90
	III	8	13.6 — 14.6	—	—
June 2	D	50	10.6 — 13.3	12.0	.90
June 13	d	4	8.6 — 10.2	—	—
	E	148	10.5 — 13.8	12.2	.10
	IV	8	14.1 — 16.5	—	—
July 12	F	32	10.9 — 13.8	12.4	.50
July 15	G	73	9.6 — 14.4	12.4	.10
Sep. 29	H	36	12.3 — 15.4	13.7	.50
Oct. 15	g	6	4.8 — 5.2	—	—
	J	1	14.7	—	—
Oct. 27	h	3**	2.1 — 2.3	—	—
	K	1	14.8	—	—
Dec. 1	j	50**#	2.4 — 2.8	2.6	.20
	k	44**	2.0 — 3.2	2.7	.50
	m	2**	3.8 — 4.2	—	—
	e	1	11.2	—	—
	M	12	13.1 — 15.2	—	—
Dec. 29	n	6	2.8 — 3.4	—	—
	o	148	3.5 — 4.7	4.2	.50
	N	23	11.5 — 18.0	14.2	.50
1951:					
Jan. 24	p	30	3.0 — 3.4	3.2	.90
	q	155	3.7 — 4.6	4.1	.30
	r	174	4.5 — 5.8	5.2	.50
	s	119	5.6 — 6.6	6.1	.50
	t	5	6.7 — 7.6	—	—
	f	4	10.8 — 11.7	—	—
	P	52	13.8 — 19.0	16.7	.02

* Mean and chi-square probability not calculated for groups of less than 15 specimens. A chi-square probability of 0.10 (10%) and above estimates with confidence that the groups are homogeneous.

** Unsexed juveniles.

Attached to pleopods of mother.

gave estimates only of the occurrence of significant deviations or the lack of deviations of any of the distributions from the normal distribution. A significant deviation was interpreted as the result of the inclusion of more than one age group within a distribution. Accordingly, the frequency distributions of the thus-established heterogeneous age groups were re-observed and subdivided into apparent smaller homogeneous groups (*i.e.*, at apparent modal breaks, or de-

TABLE 3.

Basic Statistics for Groups of Males

Date	Group ♂ II	Group ♂ I	Number of Specimens	Cephalothorax Length in Millimeters: Actual Range	Mean	P
1949:						
Oct. 16	R		48	11.9 — 16.6	14.4	.50
		1	2	13.7 — 13.9	—*	—*
		Q	1	19.2	—	—
1950:						
Feb. 24	a		6	3.7 — 5.8	—	—
	A		310	6.0 — 10.2	8.1	.50
	I		27	10.4 — 14.8	12.4	.20
		S	28	12.6 — 17.3	14.8	.09
Apr. 9	b		5	7.2 — 8.5	—	—
	B		168	8.9 — 12.4	10.4	.50
	II		20	12.5 — 15.4	13.6	.50
	T		2	16.1 — 16.4	—	—
		2	36	11.9 — 14.8	13.6	.50
		W	10	15.1 — 17.5	—	—
May 12	c		1	8.7	—	—
	C		99	9.5 — 13.4	11.5	.50
	III		2	14.2 — 14.7	—	—
		3	5	11.5 — 13.8	—	—
June 2	D		83	9.8 — 13.8	11.6	.20
		4	4	12.0 — 13.6	—	—
June 13	d		3	8.4 — 9.8	—	—
	E		153	10.0 — 13.2	11.7	.50
	IV		3	13.7 — 14.5	—	—
	V		1	16.1	—	—
		5	16	11.8 — 13.6	12.8	.20
July 12	F		22	11.1 — 13.1	12.1	.50
		6	5	11.3 — 13.6	—	—
July 15	e		1	9.2	—	—
	G		56	10.4 — 14.2	12.1	.50
	VI		1	15.3	—	—
		7	37	11.0 — 14.2	12.5	.10
		8	1	18.2	—	—
Sep. 29	H		7	12.8 — 14.6	—	—
		9	88	10.8 — 15.3	12.9	.50
		10	1	16.4	—	—
Oct. 15	J		3	13.0 — 13.8	—	—
Oct. 27	K		1	14.0	—	—
		11	12	11.9 — 14.1	—	—
		12	1	16.4	—	—
Dec. 1	M		2	12.9 — 13.3	—	—
		13	1	13.5	—	—
Dec. 29	n		6	3.3 — 3.6	—	—
	o		140	3.7 — 4.6	4.2	.50
	N		17	10.7 — 15.8	13.3	.50
		14	6	11.8 — 14.5	—	—
		15	1	16.6	—	—
1951:						
Jan. 24	p		30	3.0 — 3.6	3.4	.90
	q		146	3.6 — 4.4	4.0	.50
	r		81	4.5 — 5.1	5.0	.95
	s		121	5.2 — 6.1	5.7	.30
	t		47	6.1 — 6.8	6.4	.50
	f		10	13.4 — 13.9	—	—
	P		23	14.0 — 18.4	15.8	.90
		16	18	11.6 — 18.5	14.2	.50

* Mean and chi-square probability not calculated for groups of less than 15 specimens. A chi-square probability of 0.10 (10%) and above estimates with confidence that the groups are homogeneous.

pressions in the frequency distributions) and the chi-square test applied to each new sub-group. In the majority of cases the heterogeneous age groups could be subdivided by this procedure into homogeneous age groups with an acceptable degree of confidence.

When all lots had been subdivided into their component homogeneous age groups (Tables 2 and 3), the data were plotted as bars (actual ranges and means) on time graphs and the major facts of the annual cycle of this species were ready for interpretation. Reference to these graphs (figs. 1 and 2) will be made repeatedly in connection with the elaboration of the life cycle which follows.

THE LIFE CYCLE

Females.—The maturing females (fig. 1, series A, B, C . . . P) increased significantly in size from February to early June at which time they reached a growth plateau that was maintained through July. Between July and September another significant increase in growth was evident. Since ovigerous females were first seen in September this last increase in size is interpreted as representing the "maturity molt" of the spawning population of females and probably compares to the male maturity molt (*i.e.,* transformation from second- to first-form) which must occur prior to copulation. From September to December the mature females did not show any additional significant change in size.

The December adult females (group "N") appeared to have increased again in January forming part of group "P", indicating that at least one molt had taken place. That females molt after the young leave them was substantiated by laboratory observations. In terms of the life history this molt may be interpreted as marking the end of the active reproductive season. Tack (1941) with *Orconectes immunis* and Penn (1943) with *Procambarus clarkii* both found that females molted after their young had left, although not immediately.

Group I (fig. 1, series I-IV) is assumed to have been a continuation of a 1949 group comparable to group "f" of January 1951, and was probably about a year old. Although not represented by large numbers, this series was definitely represented in the samples through June, but by September seemed to have disappeared, reappearing presumably in December and January to form the upper ranges of groups "N" and "P".

In view of the facts that representatives of Series I-IV were not in the samples from July to December and that several large females were collected in September showing signs of having already completed spawning (*i.e.,* with remains of hatchlings' exuviae on their pleopods) it is thought that other individuals also had been ovigerous before September and had been overlooked because they were already in burrows.

Individuals of the series "Q" through "W" were not evident in the samples from April on, and it is assumed that they had died by this date. It is assumed that group "P", representing the terminus of two combined series (A-P and I-IV) which were one and two years old

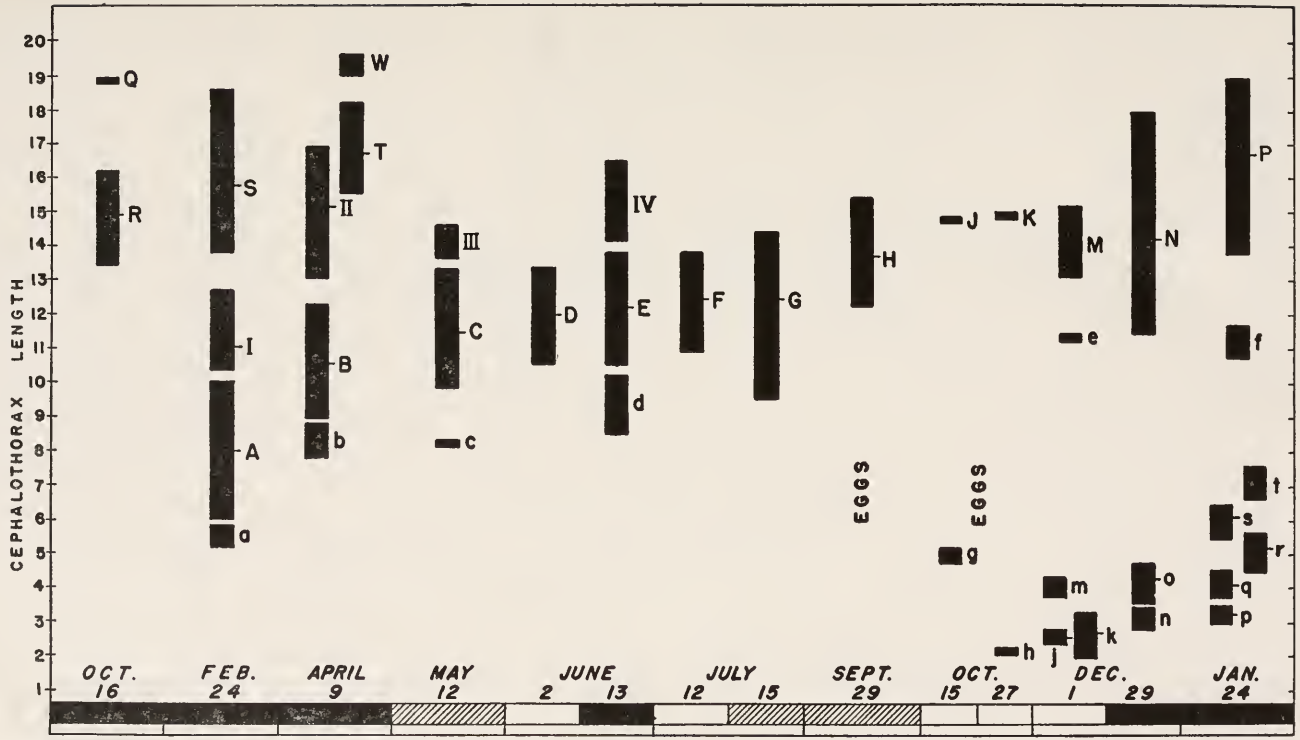


Figure 1. Females. Vertical bars represent age groups, horizontal lines represent the means of the groups. Those groups for which the means are not given contain less than fifteen individuals. Horizontal bar at bottom of graph indicates the condition of the ditch: solid = wet; cross-hatched = intermediate; open = dry.

respectively, followed the same trends as groups "Q" thru "W" and died in the spring of 1951.

The presence of various groups of juveniles (fig. 1, series a, b, c . . . f) from October through January indicates that egg maturation and embryonic development of the entire population was spread over a period of several months. The growth trends of each of these groups cannot be clearly understood from the analyses. The latest juveniles added to the free-swimming population (group "p") probably represented the offspring of the few late-spawning females found in December with young still attached to their pleopods. It is assumed that the January juvenile groups eventually gave rise to groups comparable to groups "a" and "A" of February 1950.

Males.—As might be expected the growth of the male population as a whole paralleled that of the females in most respects, but the interpretation is complicated by the shifts in groupings accompanying the maturation molt from second- to first-form. The maturing second-form males (fig. 2, series A, B, C . . . P) increased significantly from February to May; from May through July they endured a growth plateau as did the maturing females of the same time period. Sometime between May and July some of the larger second-form males apparently matured and molted to first-form, and there is evidence that the greater percentage actually transformed by May. The period from February to May was characterized by significant growth increases, and, if the male population exactly paralleled the female a maturity molt should not have occurred during this time. However, with the advent of the summer growth plateau and because of the overlap of size groups of second- and first-form males in May and June (fig. 2, groups "C" with "3", and "D" with "4") it is inferred that some of the larger second-form males had molted into first-form by May (fig. 2, group 3), and that others molted and became parts of the groups "4", "5" and "6", and most of the groups "7" and "9" when the climax of breeding was reached in September.

The majority of group "9" is thought to have continued as first-form males to December. Groups "H" through "M" represent either second-form males that had already molted back to first-form (*i.e.,* from group "3" through "7") and/or those which would molt to first-form later in January. From the statistics comparing these groups the latter assumption seems most justified.

Groups "11", "13" and "14" represent, at least in part, a continuation of group "9". By December and January, individuals of these groups molted back to the second-form and constituted the upper parts of groups "N" and "P". Those individuals of groups "N" and "P" which had not yet molted to first-form apparently did so in January and constituted the upper part of group "16".

The fact that first-form males molt back to second-form was established by laboratory observations of first-form males of the December sample, most of which had molted back to second-form by January 27th.

Group "e" (fig. 2, series a, b, c . . . e) appears to have developed by December into the lower part of group "N". By January the lower part of group "N" is thought to have molted into first-form and

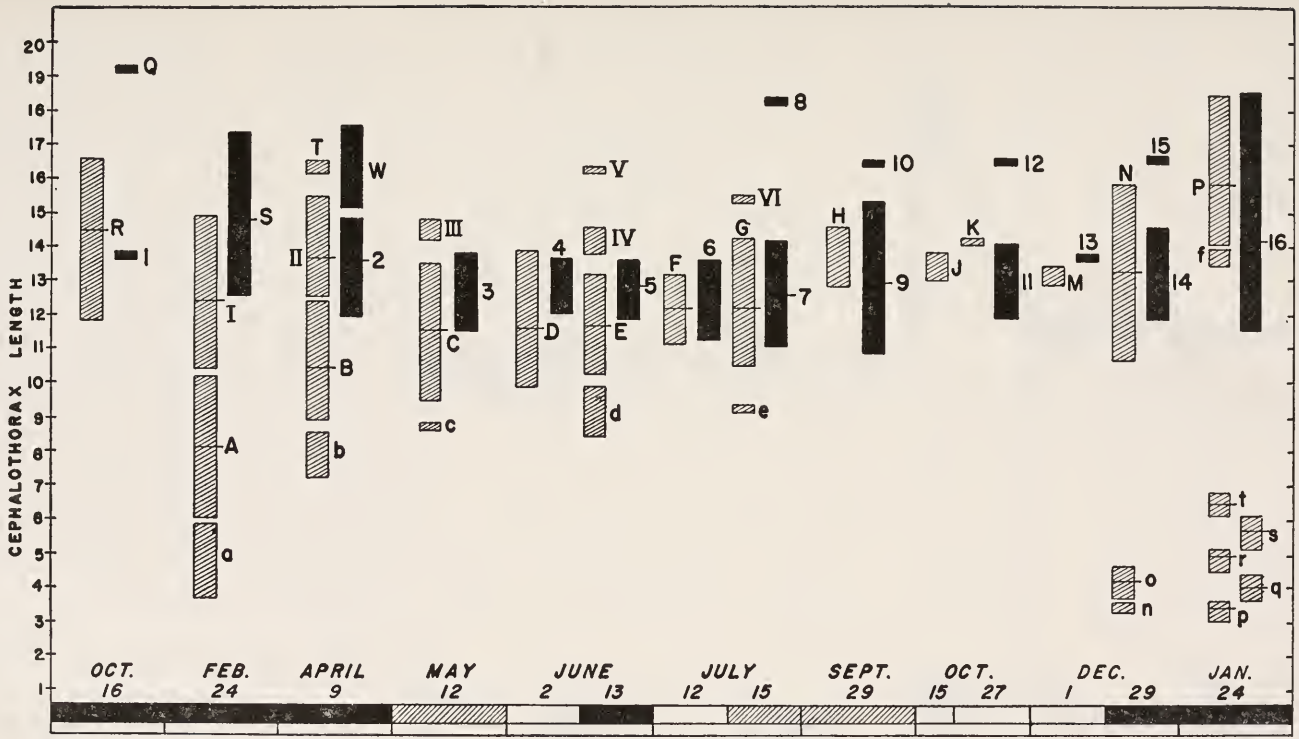


Figure 2. Males. Second-form males represented by cross-hatched bars, first-form males by solid bars. Vertical bars represent age groups, horizontal lines represent the means of the group. Those groups for which means are not given contain less than fifteen individuals. Horizontal bar at bottom of graph indicates the condition of the ditch: solid = wet; cross-hatched = intermediate; open = dry.

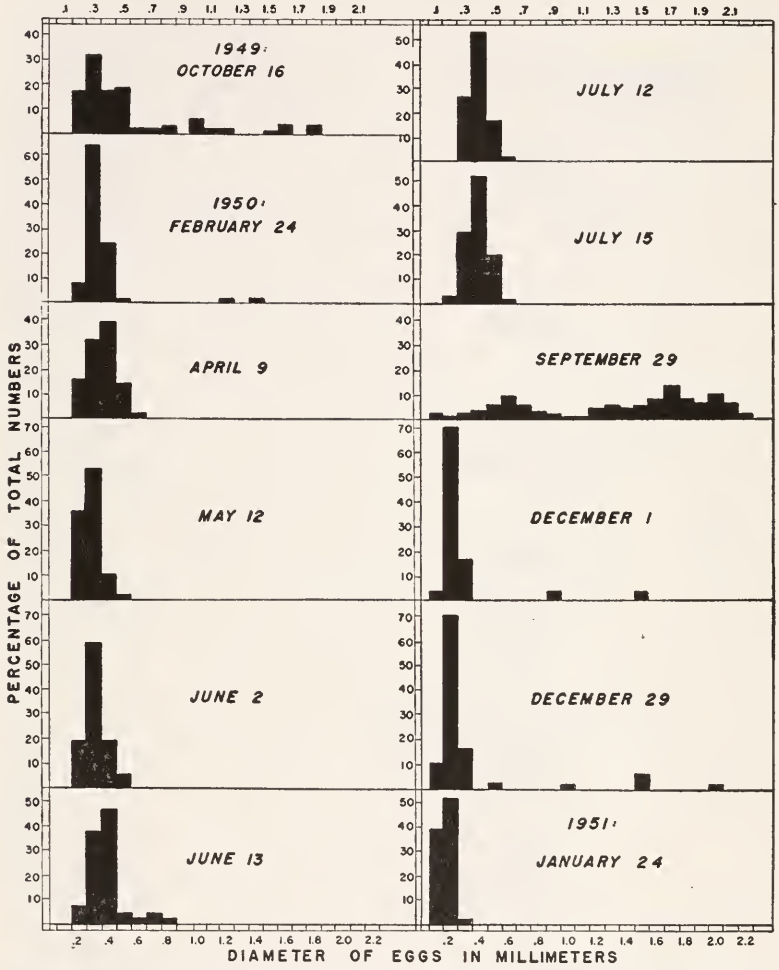


Figure 3. Maturation of ovarian eggs. Each sample is represented by a percentage frequency histogram in which each bar represents the percentage of the total number of individuals within the histogram.

then constituted at least the lower part of group "16".

Group I of February (fig. 2, series I-VI) apparently was constituted of contributions from group "R" (its upper range) and from a group comparable to group "f" of January (its lower range). Representatives of this series were in each sample from February through July 15th. Prior to February some individuals molted to first-form (group "1") and from February through July the majority also molted to first-form contributing to the groups "S" and "2" through "7". From September through December the remaining few molted to first-form and were represented by groups "10", "12" and "15".

Groups "Q" and "W" and the upper part of "S" apparently died in

the spring as indicated by the absence of the proper size in the May and June samples. The upper range of group "R" was probably composed of males recently molted from first- to second-form. Group "T" was a continuation of this group which apparently died by May.

From these conclusions the fate of the January adult group may be stated. The upper ranges of groups "P" and "16" should have died first and the remainder of these groups probably died before the next major reproductive period in 1951. Group "f" should have formed a group comparable to group "I" of February and lived to be about two years old.

The growth trends of the male juveniles (fig. 2, series n, o, p . . . t) were assumed to be essentially similar to those of the female juveniles.

Ovarian Egg Development.—The trend of ovarian egg development for the year 1950 was determined quantitatively from a comparative study of percentage frequency histograms (fig. 3) made for each sample, in which the measurements of ovarian eggs were grouped into 0.10 mm size classes.

Prior to July 12th the ovarian eggs seemed to have been static in size and in this stage did not show any tendency toward maturing at different rates as might have been expected from the study of the egg-laying and rates of development of the young.

Except for the samples of February and June 13th the upper ranges of these did not exceed 0.6 mm (fig. 3). Only two percent of the February sample fell within the higher range, and since it was concluded previously that most of the females had already undergone a molt terminating the major reproductive period, it is inferred that these larger eggs in February were eventually resorbed. Penn (1943) for *Procambarus clarkii* gave evidence that a greater number of eggs may be developed in the ovary than are laid, and Stephens (1952) showed that ovarian eggs are readily resorbed by female *Orconectes virilis* under experimental conditions.

By September the majority of the eggs were in the large size group with peaks at 1.3, 1.7 and 2.0 mm. The presence of these large eggs within the ovaries coincided with the presence of eggs on the pleopods. Within the range below 1.0 mm the peak of 0.6 mm occurred. It is thought that these eggs eventually matured and were laid.

In September another small peak was noted at the 0.10 mm size. These are believed to represent recently developed ovarian eggs of females which had already spawned prior to the date of the sample.

In October females carrying eggs were still present in the samples. Although no ovarian study was made for this month, due to the inadequacy of the sample, it is assumed that the results of the October 1949 analysis would roughly apply. Although apparently egg-laying was still in progress, the majority of the mature female population had already spawned, as indicated by the higher percentages of small eggs.

The December samples showed that at least ninety percent of the population had already laid eggs prior to this date. The large eggs still present in the ovaries represented either those that were eventually resorbed, or that were eventually laid at the individual erratic spawn-

ing times. In general composition this sample compared with that of February 1950.

By January 1951 the ovarian eggs of the females were all immature, indicating that the reproductive period for the population as a whole had definitely terminated.

The reproductive potential was determined from a total count of the ovarian eggs of all mature non-ovigerous females (nineteen) of the September sample. The average of these counts is 14.2 eggs per female within the relatively wide extremes of 9 and 21 (Table 4).

Sex Ratio and Burrowing Responses.—Although burrowing during drought was adequately confirmed by field observation, these activities could not be observed directly during the wet periods and an analysis of the sex ratio of these collections was relied on to furnish these data. It was assumed that if the water samples, which were apparently representative of the water population, did not contain the expected sex ratio, then a significant absence or predominance of one or the other sex for any particular sample would indicate a burrowing component.

The "theoretical sex ratio" was based on the actual sex ratio of the younger male and female homogeneous groups of the February 1950 sample (figs. 1 and 2, groups "A"). The sex ratio for this group was females/males=333/310 or 1.07. This group was chosen because the specimens were large enough to sex easily and all of the young population was assumed to be in the water at this time of the year. To determine the chance differences and real differences between this ratio and the sex ratio of any other group or sample, the limits of a continuum of likely hypothesis (differences due to chance) and the limits marking off two continua of unlikely hypothesis (real differences) were established from the percentage of males to females in the young February groups.

The results of the comparison (Table 5) show that the females were not significantly different from the theoretical sex ratio during the months of February and December 1950 and January 1951, and possibly April 1950. For these months either both sexes were burrowing or both were not and the fact that both sexes were responding alike obscures the issue. However, since all these samples were large in numbers and taken from the ditch during decidedly wet periods (Table 1) it is assumed that most of the population was probably in the water.

Those collections in which the percentages of females were significantly less than the theoretical ratio were the samples of October 1949 and June 13, July 15 and September 1950. Since the females were not in the water samples it is assumed that they were burrowing. Since burrowing coincided in September with the presence of large eggs in the ovaries (fig. 3) or the presence of eggs on the pleopods, it is concluded that the egg-laying activity was a stimulus to burrowing. This conclusion lends corroboration to the possibility of erratic or pre-seasonal reproductive activities of the June 13 and July 15 samples as already indicated (fig. 3) from the study of ovarian eggs.

Analyses of the samples taken from burrows indicates that with one

TABLE 4.

OVARIAN EGG PRODUCTION

Cephalothorax Length (mm)	Number of Eggs of Individual Females	Total Number of Females of Size Class	Total Number of Eggs of Size Class	Average Number Eggs per Female
13.1	11	1	11	11.0
13.3	12, 16	2	28	14.0
13.5	10, 11, 12	3	33	11.0
13.7	9, 12, 16, 20, 21	5	78	15.6
13.9	15, 15, 18	3	48	16.0
14.1	13, 14	2	27	13.5
14.3	12, 15, 18	3	45	15.0
	GRAND TOTAL	19	270	14.2

exception (July 12) there was a significant absence of females in each of the dry samples. Since it has been established that the entire population burrowed during drought there is no logical reason why the females should not have been collected except that the technic of dry sampling was inadequate. The only other conclusion would be that of a mass death of only the females during drought times and this is biologically unacceptable.

SUMMARY AND DISCUSSION OF LIFE CYCLE

During the dry periods the crawfishes burrowed along the sides of and in the bottom of the ditch instead of migrating to the adjacent slough, a permanent body of water. There was no evidence during the course of this study to indicate that the crawfish ever migrated over dry land; however, dispersal was possible and evidences of it were observed during periods of flooding rains. Ovigerous females were found in burrows regardless of the conditions in the ditch. Indeed, the first ovigerous females collected were dug from burrows alongside the flooded ditch in September. It may be significant that immediately following this observation a drought period ensued and the remainder of the population was forced to burrow. The females carrying the vulnerable eggs were thus, by natural instincts, already in protected burrows when the drought conditions began. It would seem that an ovigerous female could not be so agile or successful a burrower as one unencumbered by eggs. However, it is not known whether spawning females burrowed before or after laying their eggs.

The eggs of *O. clypeatus* are surprisingly large in comparison to the relatively small size of the females carrying them. This certainly is correlated with the low average of 14.2 eggs per female, and perhaps the whole concept is correlated with the burrow habitat of the ovigerous females. It is interesting, and possibly significant, that a very low reproductive potential also obtains in *Procambarus hageni-anus* (Faxon) in which the females similarly shun free-water when ovigerous (Lyle, 1938).

Ovigerous females were collected on September 29 and October 15, 1950. No collections at all were made in November, but females collected on December 1st were carrying young still clinging to their pleopods. Although the length of time between oviposition and hatching, and the time that females normally carry their young was not determined it is assumed that both time periods were of short duration since free-living young first appeared in the population in the October 15th sample, about two weeks after the first ovigerous females were collected.

The juveniles of January 1951 were represented by five overlapping age groups. Three groups comparable to the three larger groups of this sample probably participated in the major spawning period (September-October) of 1950. Groups comparable to the two younger groups of January 1951 may have given rise to groups that spawned erratically (*i.e.,* post-seasonal: November-December) during 1950.

As a group the maturing females increased significantly in size from February to early June. From this date until July 15th they

TABLE 5.

Sex Ratios

Date	Range	Total Crawfish	Males	Females	Percent of Females
1949:					
Oct. 16	All	68	51	17	25
1950:					
Feb. 24	Adults	122	55	67	55
	Juveniles	654	316	338	52
Apr. 9	All	453	240	213	47
May 12	All	192	107	85	44
June 2	All	137	87	50	36
June 13	All	340	184	156	46
July 12	All	59	27	32	54
July 15	All	169	96	73	43
Sep. 29	All	131	95	36	27
Dec. 29	Adults	47	24	23	49
	Juveniles	300	146	154	51
1951:					
Jan. 24	Adults	107	51	56	52
	Juveniles	848	389	459	54

remained nearly static in size, but between mid-July and September they again increased significantly in size, presumably undergoing a maturity molt. Another molting period ensued during December and January marking the termination of the active reproductive period for the majority of the mature females. Apparently most of these females lived about a year and a half, dying before the next major spawning period. The females that were already a year old in early 1950 probably constituted an erratic pre-seasonal (July-August) spawning group in 1950 and died in the first months of 1951 at an age of about two years.

As a group the males were similar to the females in growth patterns. The maturing second-form males increased significantly in size until May at which time the growth plateau was reached. During May a few of this group molted into first-form males. By September the majority of them molted into first-form except the very youngest. These latter apparently transformed towards the end of December and formed an erratic post-seasonal spawning group among the males. Many of the first-form males molted back to second-form during December and January. The participants of the major spawning group lived to be about one year old, while the participants of the post-seasonal spawning period lived to be about two years old.

ACKNOWLEDGEMENTS

The writer is deeply indebted to Dr. George Henry Penn under whose direction this study was made. She is particularly grateful for his help on many of the field trips and especially for the collections of June and July which he made; for his many helpful suggestions during the laboratory exploration, and for his guidance and encouragement in the presentation of this paper. She is also indebted to Prof. Joseph A. Ewan, of the Department of Botany of Tulane University, for the identification of the plants in the ditch, and to Messrs. Lothar E. Hornuff, Jr. and Edward N. Lambremont for their assistance on several field trips.

REFERENCES CITED

Bovbjerg, Richard V. 1952. Comparative ecology and physiology of the crayfish *Orconectes propinquus* and *Cambarus fodiens*. *Physiol. Zool.*, 25 (1): 34-56.

Cazier, Mont A. and Annette L. Brown 1949. Introduction to quantitative systematics. *Bull. Amer. Mus. Nat. Hist.*, 93 (5): 343-388.

Creaser, Edwin P. 1933a. Seasonal changes in the male population of *Faxonius propinquus* (Girard). *Occ. Pap. Mus. Zool. Univ. Mich.*, No. 253: 1-9.

---------- 1933b. Descriptions of some new and poorly known species of North American crayfishes. *Occ. Pap. Mus. Zool. Univ. Mich.*, No. 275: 1-21.

Creaser, E. P. and A. I. Ortenburger 1933. The decapod crustaceans of Oklahoma. *Publ. Univ. Okla. Biol. Surv.*, 5 (2): 14-47.

Faxon, Walter 1914. Notes on the crayfishes in the United States National Museum and the Museum of Comparative Zoology with descriptions of new species to which is appended a catalogue of the known species and subspecies. *Mem. Mus. Comp. Zool.*, 40 (8): 347-427.

Hay, W. P. 1899. Description of two new species of crayfish. *Proc. U. S. Nat. Mus.*, 22: 121-123.

Hobbs, Horton H., Jr. 1942. The crayfishes of Florida. *Univ. Fla. Publ., Biol. Sci. Ser.*, 3 (2): 1-179.

Lyle, Clay 1938. The crawfishes of Mississippi, with special reference to the biology and control of destructive species. (Abstract). *Iowa State Coll. Jour. Sci.*, 13 (1): 75-77.

Peatman, John G. 1947. *Descriptive and Sampling Statistics*. New York: Harper and Bros., pp. 1-577.

Penn, George Henry 1942. Observations on the biology of the dwarf crawfish, *Cambarellus shufeldtii* (Faxon). *Amer. Midl. Nat.*, 28 (3): 644-647.

---------- 1943. A study of the life history of the Louisiana red-crawfish, *Cambarus clarkii* Girard. *Ecology*, 24 (1): 1-18.

---------- 1952. The genus *Orconectes* in Louisiana. *Amer. Midl. Nat.*, 47 (3): 743-748.

Stephens, Gwen J. 1952. Mechanisms regulating the reproductive cycle in the crayfish, *Cambarus*, I. The female cycle. *Physiol. Zool.*, 25 (1): 70-84.

Tack, Peter Isaac 1941. The life history and ecology of the crayfish *Cambarus immunis* Hagen. *Amer. Midl. Nat.*, 25 (2): 420-446.

Van Deventer, William C. 1937. Studies on the biology of the crayfish *Cambarus propinquus* Girard. *Illinois Biol. Monogr.*, 15 (3): 1-67.

[N.A.-New Orleans]

TULANE STUDIES IN ZOOLOGY

Volume 1, Number 8 December 21, 1953

OSTRINCOLA GRACILIS C. B. WILSON, A PARASITE OF MARINE PELECYPODS IN LOUISIANA

(COPEPODA, CYCLOPOIDA)

ARTHUR G. HUMES,

DEPARTMENT OF BIOLOGY, BOSTON UNIVERSITY, BOSTON, MASSACHUSETTS.

MUS. COMP. ZOOL. LIBRARY

JAN 4 1954

HARVARD UNIVERSITY

TULANE UNIVERSITY

NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico and the Caribbean Sea. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

TREVOR KINCAID, Emeritus Professor of Zoology, University of Washington, Seattle, Washington.

ROBERT W. PENNAK, Professor of Zoology, University of Colorado, Boulder, Colorado.

HARRY C. YEATMAN, Assistant Professor of Biology, University of the South, Sewanee, Tennessee.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

When citing this series authors are requested to use the following abbreviations: *Tulane Stud. Zool.*

Price for this number: $0.25.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University,
New Orleans, U. S. A.

MUS. COMP. ZOOL.
LIBRARY
JAN 4 1954
HARVARD
UNIVERSITY

OSTRINCOLA GRACILIS C. B. WILSON, A PARASITE OF MARINE PELECYPODS IN LOUISIANA

(COPEPODA, CYCLOPOIDA)

ARTHUR G. HUMES,[1]

Department of Biology, Boston University, Boston, Massachusetts.

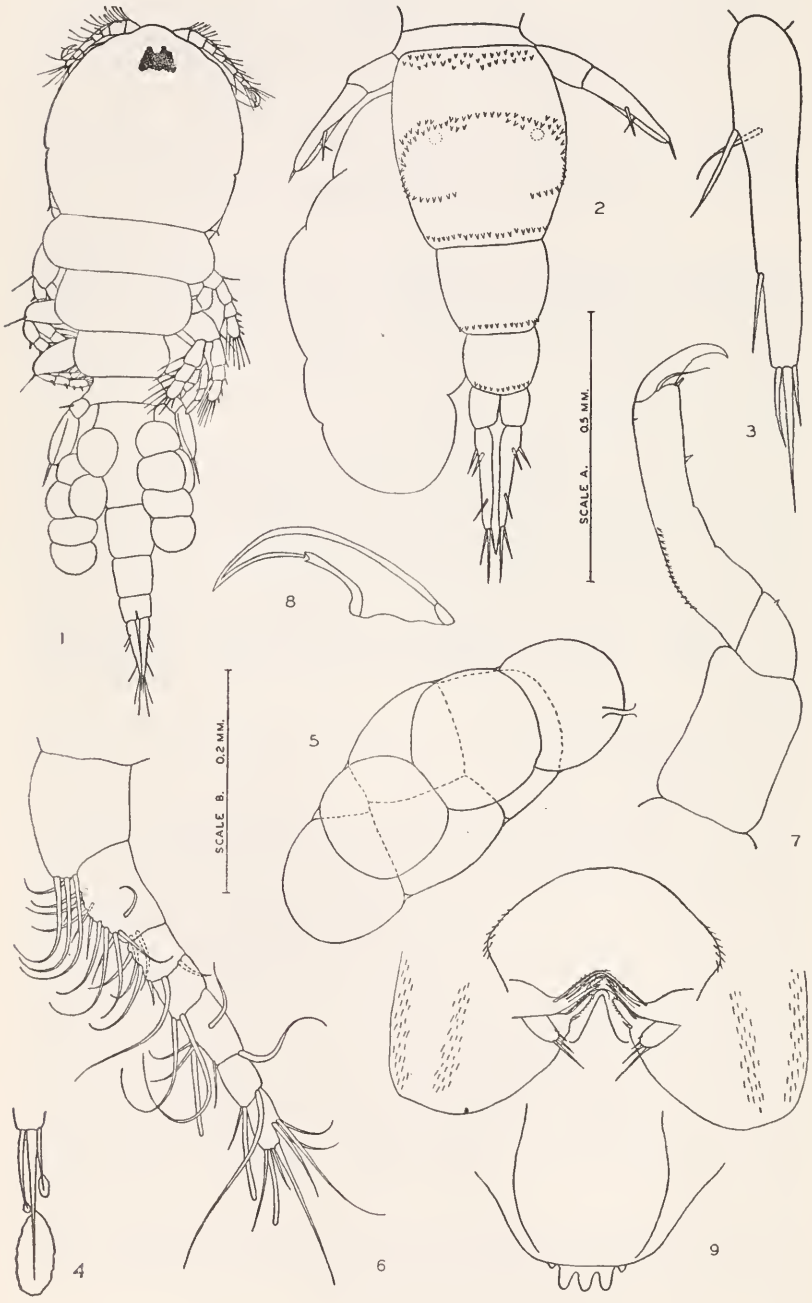
In June, 1947, a parasitic copepod, *Ostrincola gracilis* C. B. Wilson (1944), was discovered in the mantle cavity of four species of pelecypods from the Barataria Bay region of Louisiana. The hosts were the Virginia oyster (*Crassostrea virginica* Gmelin), the ribbed mussel (*Modiolus demissus granosissimus* Sowerby), the recurved mussel (*Mytilus recurvus* Rafinesque), and the hard shelled clam or quahaug (*Venus mercenaria mercenaria* Linné.).

A study of the copepods thus obtained has revealed certain important omissions and inaccuracies in the original description. The holotype and allotype specimens, U. S. National Museum No. 79697, have not been available for dissection and study, but a male and a female, U. S. National Museum No. 79698, having the same collection data as the holotype and allotype and apparently paratypes though not designated as such by Wilson, have been compared in detail with the Louisiana forms. The specimens from Louisiana proved to be conspecific with the actual specimens of *O. gracilis* as identified by Wilson.

For helpful suggestions in connection with this paper I am indebted to Mrs. Mildred S. Wilson.

Female.—The body (fig. 1) in living specimens is colorless, except for a dark reddish-black median eye and a brownish intestine. (In glycerine and polyvinyl alcohol mounts the eye is bluish.) The total length (from the tip of the head to the posterior end of the caudal rami), based on an average of five specimens, is 1.083 mm and the greatest width of the cephalothorax is 0.274 mm. The abdomen is three-segmented. The ventral surface of the genital segment and abdomen bears minute spines arranged as in figure 2, but the dorsal surface lacks spines. The caudal ramus (fig. 3) bears three terminal setae and three along its outer edge. The terminal setae in many specimens show brownish accretions around their tips (fig. 4). The egg sacs (fig. 5) both contain about seven eggs and are attached dorsolaterally. The first antenna (fig. 6) has seven podomeres and bears several aesthetes. The arrangement of the setae on the distal podomere suggests a subdivision into two podomeres

[1] The material upon which this paper is based was collected while the author was a guest investigator at the Louisiana State University Marine Laboratory at Grand Isle, Louisiana.


1
2
3
4
5
6
7
8
9
SCALE A. 0.5 MM.
SCALE B. 0.2 MM.

but there is no articulation. The second antenna (fig. 7) has a notch-like interruption on the inner margin of the claw (fig. 8).

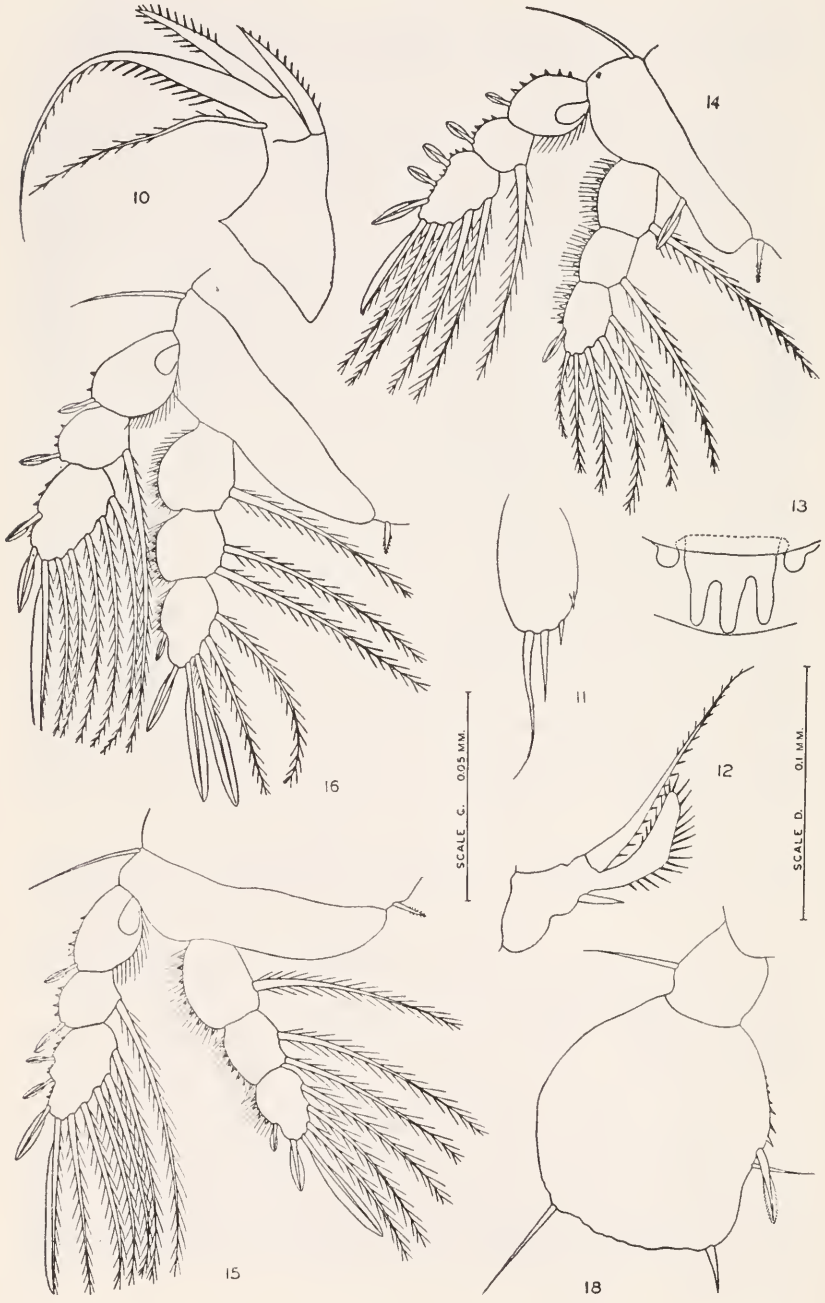
The mouthparts (fig. 9) are much reduced. The labrum is wider than long and bears on each side a group of small spines. Its posterior edge seems to be entire and not deeply incised, although this feature is difficult to ascertain because of the impinging of the labrum and the mouthparts. The mandible (fig. 10) has a somewhat elongated base with an apical armature of four elements. The first maxilla (fig. 11) is minute and arises from a point along the distal half of the basal part of the mandible. In unmounted specimens the first maxillae extend nearly vertically from the ventral body surface, but in pressed whole mounts they appear to be directed more posteriorly. Each first maxilla consists of a single lobe bearing four setae which are progressively shorter toward the midline of the body. The second maxilla (fig. 12) has a much inflated basal part and a relatively small apex with tripartite armature. The distal portions of both the mandibles and the second maxillae in unmounted specimens are directed vertically from the ventral body surface and somewhat anteriorly. The mandibles and both pairs of maxillae are minute and closely appressed, so that it is only with great care that they can be isolated for study. The labium is small and rather poorly delimited, with a longitudinal concavity on its posterior surface. The maxillipeds are lacking. In the median region of the head posterior to the labium there is a prominent postoral protuberance, especially conspicuous in lateral view. In the midline of the body on the anterior surface of the ridge between the bases of the first pair of legs there is a trilobed structure (fig. 13). In pressed specimens this trilobed area appears to be overlapped by the posterior edge of the postoral protuberance.

The first, second, third, and fourth swimming legs are shown in figures 14-17 respectively. The spine and setal formula is as follows:

	leg 1		leg 2		leg 3		leg 4	
	exp	end	exp	end	exp	end	exp	end
first podomere	1:0	0:1	1:0	0:1	1:0	0:1	1:0	0:1
second podomere	1:1	0:1	1:1	0:2	1:1	0:2	1:1	0:2
third podomere	8	6	9	6	8	6	8	5

The fifth leg (fig. 18) has two podomeres, the proximal one small with a single outer seta, the distal one expanded into a broad, in-

Figures 1-9. *Ostrincola gracilis*, female: **1**, dorsal view; **2**, genital segment and abdomen, ventral view; **3**, caudal ramus; **4**, terminal setae of caudal ramus with accretions; **5**, egg sac; **6**, first antenna; **7**, second antenna; **8**, detail of claw of second antenna; **9**, area of mouthparts.


10
14
13
11
12
16
15
18
SCALE C. 0.05 MM.
SCALE D. 0.1 MM.

wardly concave disk with four marginal setae.

Male.—The color in life resembles that of the female. The total length, based on an average of five specimens, is 0.760 mm and the greatest width of the cephalothorax is 0.200 mm. The abdomen is four-segmented (fig. 19). The ventral surface of the genital segment and abdomen bears minute spines as in figure 20. The caudal rami are like those of the female. The first antenna (fig. 21) has seven podomeres, with all but the proximal one having an aesthete.

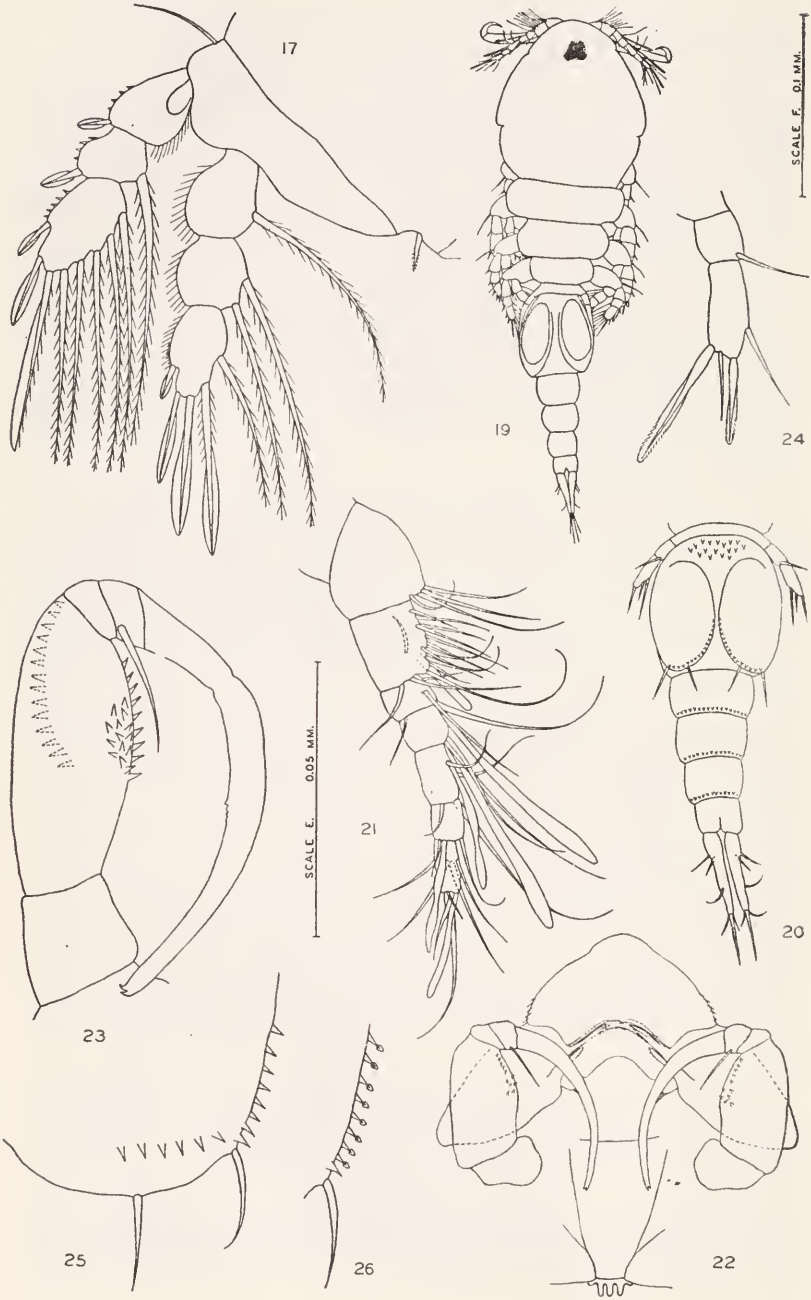
The second antennae, mandibles, first maxillae, and second maxillae are like those of the female. The maxilliped (figs. 22, 23) has five podomeres, the proximal one short, the second large and spinose on its outer and inner margins, the third short, the fourth short also with an inner seta, and the last elongated, arcuate, and slender. The last podomere is as long as or slightly longer than the rest of the podomeres together.

The four pairs of swimming legs are identical in structure with those of the female, having the same spine and setal arrangement. The fifth leg (fig. 24) has two podomeres, the first with a single outer seta, the second longer, not expanded, but with more or less parallel margins, and with four marginal setae. The sixth leg (figs. 20, 25) consists of two setae at the posterior corner of the genital segment. In a few males some of the spines near the sixth legs show brownish caps covering their tips (fig. 26).

Remarks.—*Ostrincola* seems to stand between the ergasilid genus *Myicola* Wright (1885) and the Lichomolgidae as represented by the genus *Pseudomyicola* Yamaguti (1936). The segmentation and armature of the first antenna, the mandible, the first and second maxilla, the male maxilliped, and the segmentation and armature of legs 1-4 resemble *Myicola metisiensis* Wright. In two respects at least *Ostrincola* differs from *Myicola.* The second antenna is rather elongated and slender, while in *Myicola* it is shortened and robust. The distal podomere of the fifth leg in the female is much expanded, while in *Myicola* it has nearly subparallel margins. In both these characters *Ostrincola* resembles the condition in *Pseudomyicola,* differing from that genus, however, in the first antenna, the mandible, and other features.

The generic validity of *Ostrincola* seems to rest upon the future discovery of other related species. In the meantime, however, the original generic description may be emended as follows:

Figures 10-16, 18. *Ostrincola gracilis,* female: **10,** mandible; **11,** first maxilla; **12,** apex of second maxilla; **13,** trilobed structure between bases of first legs; **14,** first leg; **15,** second leg; **16,** third leg; **18,** fifth leg.


17
19
24
SCALE F. 0.1 MM.
21
SCALE E. 0.05 MM.
20
23
25
26
22

OSTRINCOLA Wilson 1944, *emended diagnosis*

Body cyclopoid with head and first thoracic segments fused. Thoracic segments 2-5 diminishing regularly in width. Genital segment longer than wide. Abdomen three-segmented in the female, four-segmented in the male. Caudal rami much elongated and subcylindrical. Sexual dimorphism not pronounced. Attachments of egg sacs dorsolateral; eggs relatively few in number.

First antenna in both sexes with seven podomeres. Second antenna uniramous, with four podomeres, the penultimate relatively long and slender and the last a curved claw. Mandible with a moderately long basal portion bearing an apical armature of four parts, directed anteriorly. First maxilla a minute somewhat posteriorly directed lobe arising from the area immediately behind the distal half of the base of the mandible and bearing four unequal setae. Second maxilla with a much inflated basal part and a small apical portion with tripartite armature, directed anteriorly. Anterior to the mouthparts a swollen labrum without a deeply incised posterior edge, and posterior to them a rather weakly developed labium. Behind the labium a swollen postoral protuberance. Maxillipeds lacking in the female. The male maxilliped large, with five podomeres, the second podomere elongated and relatively stout, the last podomere slender, arcuate, and about as long as the other four podomeres together.

Legs 1-4 biramous, the rami with three podomeres, and the spine and setal formula as in *Myicola.* Fifth leg uniramous in both sexes, with two podomeres; the distal podomere in the female expanded into a broad, inwardly concave disk armed along the margin with four setae, in the male elongated with subparallel margins, similarly armed.

Genotype.—*Ostrincola gracilis* Wilson 1944.

The major points in the emendation concern the number of abdominal somites, the number of first antennal podomeres, the nature of the mouthparts, and the number of podomeres in the fifth legs.

Occurrence.—In Barataria Bay *O. gracilis* was found near Chene Fleurie in *Mytilus* and *Crassostrea.* in Sugarhouse Bend Bayou at Grand Terre in *Mytilus* and *Crassostrea,* and in the tidal marsh back of Grand Isle in *Venus, Crassostrea,* and *Modiolus.* The collection data are summarized in Table 1.

Figures 17, 19-26. *Ostrincola gracilis,* female: **17,** fourth leg. Male: **19,** dorsal view; **20,** genital segment and abdomen, ventral view; **21,** first antenna; **22,** area of mouthparts; **23,** maxilliped; **24,** fifth leg; **25,** sixth leg; **26,** setae of sixth leg with cap-like coverings.

TABLE 1

INCIDENCE OF *Ostrincola gracilis* IN PELECYPODS OF THE BARATARIA BAY REGION OF LOUISIANA.

Clam Host	Number Examined	Number with *O. gracilis*	Percent Parasitized	Average Number Per Host
Crassostrea virginica	399	157	39.3	1.88 (1-11)
Modiolus demissus granosissimus	241	89	36.9	1.73 (1-7)
Mytilus recurvus	45	7	15.5	1.14 (1-2)
Venus mercenaria mercenaria	1	1	100	2
	686	254	37.0	1.81 (1-11)

Ecological notes concerning the four species parasitized are to be found in the publication of Harry (1942). According to observations previously made (Humes, 1942) the water in Barataria Bay seldom exceeds ten feet in depth, except in the passes leading to the open Gulf. The bottom is largely composed of sand and silt with extensive areas devoted to oyster beds. The summer water temperature ranges from 25.8 to 29.8° C. The salinity at Chene Fleurie is 9.18 grams per liter, while at the eastern end of Grand Terre near Sugarhouse Bend Bayou it is 25.30. Although no ecological information was given by Wilson (1944) regarding the type specimens at Beaufort, North Carolina, it seems probable on the basis of the Louisiana material that this copepod will be found as a parasite in pelecypods living in shallow-water, estuarine regions which are protected from the open sea.

EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida. Scale **A** applies to figures 1 and 19; scale **B** to figures 2, 5, and 20; scale **C** to figures 3, 4, 13, 23, 25, and 26; scale **D** to figures 6, 7, 14-18, 21, and 24; scale **E** to figures 8, and 10-12; and, scale **F** to figures 9 and 22.

REFERENCES CITED

HARRY, HAROLD W. 1942. List of Mollusca of Grand Isle, Louisiana, recorded from the Louisiana State University Marine Laboratory, 1929-1941. *Occ. Pap. Marine Lab., La. State Univ.*, No. 1: 1-13.

HUMES, ARTHUR G. 1942. The morphology, taxonomy, and bionomics of the nemertean genus *Carcinonemertes*. *Illinois Biol Monogr.*, 18 (4): 1-105.

WILSON, C. B. 1944. Parasitic copepods in the United States National Museum. *Proc. U. S. Nat. Mus.*, 94: 529-582.

WRIGHT, R. R. 1885. On a parasitic copepod of the clam. *Amer. Nat.*, 19 (2): 118-124.

YAMAGUTI, S. 1936. Parasitic copepods from mollusks of Japan, I. *Jap. Jour. Zool.*, 7 (1): 113-127.

TULANE STUDIES IN ZOOLOGY

Volume 1, Number 9 February 8, 1954

HYBRID INVIABILITY BETWEEN *RANA PIPIENS* FROM WISCONSIN AND MEXICO

E. PETER VOLPE,

DEPARTMENT OF BIOLOGY, NEWCOMB COLLEGE, TULANE UNIVERSITY, NEW ORLEANS, LOUISIANA

FEB 18 1954

HARVARD UNIVERSITY

TULANE UNIVERSITY

NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico and the Caribbean Sea. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

VICTOR C. TWITTY, Professor of Zoology, Stanford University, Stanford University, California.

JOHN A. MOORE, Professor of Zoology, Columbia University, New York, New York.

ALBERT P. BLAIR, Associate Professor of Zoology, University of Tulsa, Tulsa, Oklahoma.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

When citing this series authors are requested to use the following abbreviations: *Tulane Stud. Zool.*

Price for this number: $0.35.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University,
New Orleans, U. S. A.

LIBRARY
FEB 18 1954

HYBRID INVIABILITY BETWEEN *RANA PIPIENS* FROM WISCONSIN AND MEXICO[1]

E. PETER VOLPE,

Department of Biology, Newcomb College, Tulane University, New Orleans, Louisiana

Laboratory crosses among individuals of various populations of the widely-distributed meadow frog, *Rana pipiens,* have revealed the extent to which intraspecific gene exchange is possible. The occurrence of abnormalities in hybrids between certain geographical populations of *R. pipiens* has been demonstrated by Moore (1949a). In general, the intensity of hybrid defects is inversely proportional to the north-south distance between the localities of the parents employed in the laboratory hybridizations. It has also been shown (Moore, 1949b) that the geographically extreme northern and southern populations of this species differ in embryonic rate of development and embryonic temperature tolerance. Moore has inferred that these embryological differences represent differential adaptations to environmental temperatures, and he further surmises that the embryonic defects in hybrids between northern and southern individuals may be associated with the different temperature adaptations of the parental eggs.

The most severe abnormalities have been observed in hybrids between *R. pipiens* from Alburg, Vermont and two localities in eastern Mexico, Monterrey in Neuvo Leon and Axtla in San Luis Potosi (Moore, 1947).

In the present investigation, meadow frogs obtained simultaneously from a different northern locality, Oshkosh, Wisconsin and several localities in the State of Tamaulipas, Mexico provided the opportunity to hybridize the respective groups, and thus contribute additional information on the problem of geographical differentiation and the development of isolating mechanisms in populations of *R. pipiens*.

Experimental

A comparison was made of the rate of embryonic development and embryonic temperature tolerance of *R. pipiens* from Mexico and Wisconsin to determine if differences existed, and reciprocal hybrid crosses were conducted to ascertain the extent of developmental compatibility. The methods of experimentation were essentially similar to those employed in other work of this type (Moore, 1946, 1949b; Volpe, 1952, 1953). The technique, and the modifications introduced, will be brought out during the discussion of the experiments.

Embryonic temperature adaptations.—Ovulation of Mexican and Wisconsin meadow frogs was induced by pituitary injection. The

[1] Aided by a grant from the Tulane University Council on Research. I am indebted to Dr. R. M. Darnell of Tulane University for collecting the meadow frogs from Mexico, and to Miss Vera Morel for the drawings used in illustrating this paper.

eggs were stripped from the females into sperm suspensions prepared by macerating the testes of a male in 10-20 cc. of 0.1% Ringer's solution. Eight artificial fertilizations, in groups of two, were conducted. Each fertilization of a Mexican ♀ X Mexican ♂ was carried out simultaneously with a cross Wisconsin ♀ X Wisconsin ♂. By conducting parallel fertilizations, differences in rate of development of Mexican and Wisconsin embryos were readily apparent. The four ovulated Mexican females were derived from four different localities, as follows: (1) Storm's Ranch, 7 km. northeast of Gomez Farias, Tamaulipas; (2) La Union, 9½ km. north of Gomez Farias, Tamaulipas; (3) El-Mante-Tampico Highway, 29 km. east of El Mante, Tamaulipas; (4) El Mante-Tampico Highway, 72 km. east of El Mante, Tamaulipas. All four Wisconsin mating pairs employed came from Oshkosh, Wisconsin.

The egg masses from any single fertilization were cut into small clusters of 9 to 13 eggs to permit more surface for respiration. The eggs clusters were placed in finger bowls, each finger bowl containing ten clusters (referred to as a "group") in 200 cc of 0.1% Ringer's solution. The finger bowls were than distributed to constant temperature units, which maintained temperatures accurate to ±0.2°C. Development of four groups of Wisconsin eggs and four groups of Mexican eggs was observed at 18.9°C., 21.1°C., 27.5°C., 29.5°C., and 33°C.

The eggs derived from the Mexican females were larger than those obtained from the Wisconsin females. Measurements of the eggs (vitellus diameter) prior to first cleavage were made by means of an ocular micrometer calibrated from a 1/100 millimeter-ruled stage micrometer. The diameters of 86 Wisconsin eggs ranged from 1.60 mm. to 1.95 mm., the mean and standard deviation being 1.73±0.08. Similar measurements of 101 Mexican eggs indicated a range of 1.95 mm. to 2.20 mm. (2.10±0.06). The difference is significant (the difference of the means is three times the standard error of the difference). Although a few of the Wisconsin eggs approached the size of the Mexican eggs, a *cluster* of the latter could be readily distinguished with the unaided eye from a *cluster* of the former. This detectable difference in egg size (recall the relation of the volume of a sphere to its radius) made it possible to keep both the Mexican and Wisconsin clusters of eggs in the same finger bowl containing Ringer's solution at a desired temperature. This procedure reduced the error of developmental deviations due to any temperature variations which may have been encountered if each group of eggs had been kept in separate finger bowls. No difficulty was experienced in identifying the two groups of eggs while they developed within the jelly membranes. To obviate any difficulty in later development, the embryos of each group just prior to hatching were separated into individual finger bowls containing fresh 0.1% Ringer's solution which previously had been brought to the desired temperature.

TABLE 1.

A Comparison of Development in Eggs of *Rana pipiens* from Mexico and Wisconson

Age in hours between Stages 3 and 20

Experiment 1 18.9°C.			Experiment 2 18.9°C.			Experiment 3 21.1°C.			Experiment 4 21.1°C.		
Age in Hours	La Union, Mex. (110)[a]	Oshk., Wisc. (104)	Age in Hours	El Mante 29 km. e, Mex. (115)	Oshk., Wisc. (111)	Age in Hours	Storms Ranch, Mex. (111)	Oshk., Wisc. (105)	Age in Hours	El Mante 72 km. e, Mex. (116)	Oshk., Wisc. (109)
0	3[b]	3	0	3	3	0	3	3	0	3	3
11.0	7	7	18.2	9	9	6.0	7	7	8.2	8	8
13.2	8	8	24.5	10L	11E	13.5	9	9	18.2	11E	10M
16.2	9	9	31.2	12E	12L	16.5	10E	10E	24.2	12M	12E
20.5	10E[c]	10E	40.5	13E	13M	23.2	12E	11M	29.0	13E	12L
32.5	12M	12L	44.0	13L	14E	26.5	12L	12M	31.5	13M	13E
38.5	12L	13E	46.5	14E	14M	38.7	14L	14M	35.0	14M	14E
44.5	13L	14E	49.2	14M	14L	41.0	16E	14L	47.2	16L	16M
56.7	16E	16M	52.2	15	16E	45.5	16M	16E-M	55.0	17E-M	17E
64.0	16L	17E	64.5	16L	17E	50.5	16L	16M	66.2	18M-L	18E-M
70.5	17M	17L	70.5	17M	17L	64.0	18M	18E	69.5	18L	18M
81.0	18E	18M	76.7	17L	18E	71.5	19E	18L	78.0	19M-L	19E
93.0	19E	19M	91.2	18L	19E	76.2	19L	19E	80.0	20E	19L
96.7	19M	19L	95.0	19E	19M-L	79.0	20E	19L	83.0	—	20E
101.0	19L	20E	98.5	19M	19L	82.5	—	20E			
105.0	20E	—	102.0	19L	20E						
			104.7	20E	—						

[a] The number in parentheses indicates the number of embryos examined.

[b] The embryos were considered to be in a given stage when 50 percent or more of them exhibited the characteristics for that stage.

[c] The stages are described in Pollister and Moore (1937); the letters **E**, **M**, and **L** signify early, middle and late.

The rate of development was determined by examining the groups of embryos at each of the constant temperatures at frequent intervals from first cleavage to gill circulation. Certain problems arise in obtaining an adequate measure of the time required by a group of embryos to reach a given stage. Even when special precautions are taken to provide as uniform an environment as possible, eggs within a group exhibit variation in the speed with which they reach a given point in development. Thus, to permit statistical comparison between two groups of developing eggs, it would be desirable to make repeated observations to determine when 100 percent of the eggs had reached a particular morphological stage. This is laborious and tedious and even if this procedure were practical, it would be necessary to break the continuous embryonic development into a series of extremely minute discontinuous steps to permit an accurate determination of the extent of variation. The problem was attacked by selecting morphological stages at which recognizable specific processes begin, and the onset of a given stage was taken as the time at which 50 percent or more of the eggs within a group entered that stage. The stages drawn up by Pollister and Moore (1937) were employed, with the further refinement of designating the stages as early (E), middle (M), and late (L). In comparing two groups of eggs which were developing at different speeds, an estimate of the variability was obtained by noting the percent of embryos in the more slowly developing group which were as advanced as the majority of embryos in the second group which exhibited the faster rate of development. In all experiments, it was found that only five percent or less of the more slowly developing group of embryos were as advanced as the majority (50 percent or more) of the faster developing group of embryos; nor were there more than five percent of the faster developing group of embryos in as early a stage as the majority (50 percent or more) of the more slowly developing group of embryos. Moreover, the arbitrary criterion of 50 percent was found to be a conservative figure. From fertilization to stage 17 (tail bud stage) 80 percent or more of the embryos reached a given stage simultaneously; from stage 18 (muscular contraction) onward, 70 percent or more of the embryos entered a particular stage at the same time. Thus, although it is difficult to analyse the spectrum of variation, the ascertainment at any one reading of the norm of a group and the extreme variants of that group (in relation to the other group being compared) permits an accurate determination of comparative rates of development.

No differences could be detected in the rate of development of the four groups of Mexican embryos at each of the experimental temperatures. However, the groups of Mexican embryos differed in rate of development from those derived from Wisconsin. In Table 1 a comparison is made of the time in hours required by 50 percent or more Mexican and Wisconsin embryos within a group to reach the experimental end-point, stage 20, at two temperatures, 18.9°C

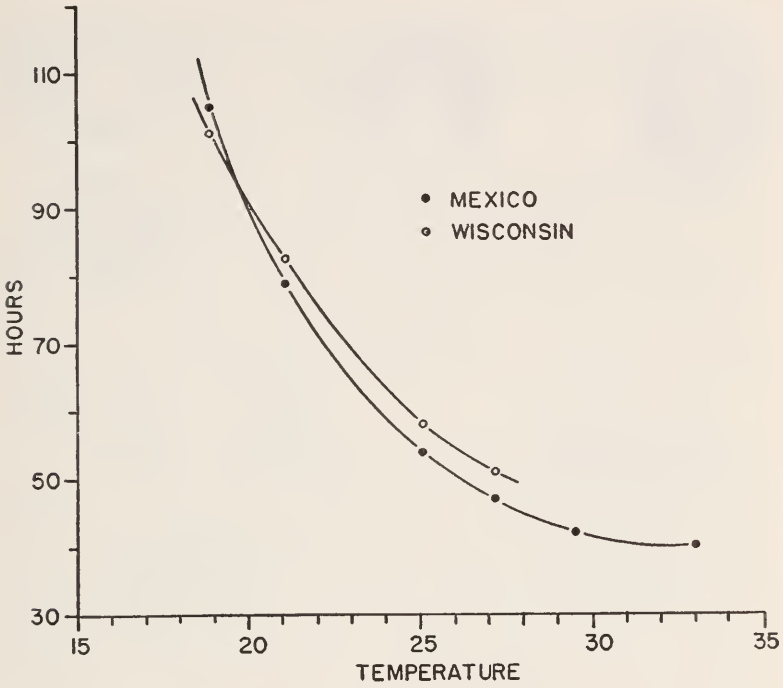


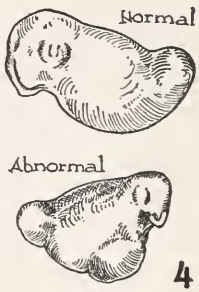
Figure 1. A comparison of the mean time, in hours, between stages 3 and 20 at different temperatures, in degrees Centigrade, of embryos of *Rana pipiens* from Mexico and Wisconsin.

and 21.1°C. At 18.9°C, the embryos from each of the different localities in Mexico developed more slowly than the Wisconsin embryos. At 21.1°C. (and higher temperatures), the Mexican embryos developed more rapidly. Figure 1 shows a plot of the mean time in hours between stages 3 and 20 required by four groups of Mexican embryos and four groups of Wisconsin embryos at the different temperatures employed. The faster rate of development of Mexican embryos at higher temperatures may be associated with the greater tolerance of these embryos to high temperatures.

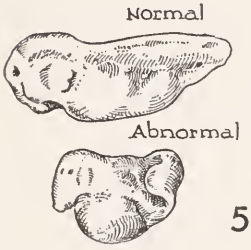
To estimate temperature tolerance, records were made of the types and proportions of embryonic abnormalities at each temperature. The Mexican embryos are decidedly better adapted to the higher temperatures. At 33.0°C, early death of all of the Wisconsin embryos was evidenced by irregular cleavage furrows. At this same temperature, the Mexican eggs cleaved normally, but the majority of the eggs later exhibited defects in gastrulation. However, an average of 13 percent for the four groups of embryos (57 of a total of 437 eggs) developed to the gill circulation stage (stage 20). At 29.5°C,

2

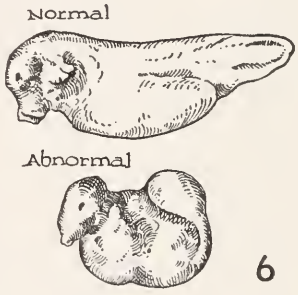
3



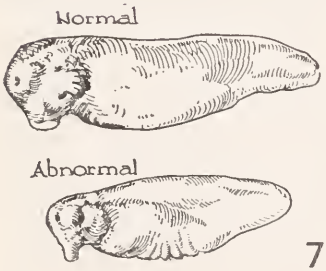
4



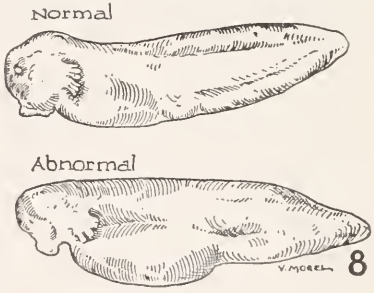
5



6



7



8

Figures 2-8. Development of hybrid embryos from the cross La Union, Mexico ♀ X Oshkosh, Wisconsin ♂. Control embryos (La Union, Mexico ♀ X La Union, Mexico ♂) are shown in some figures for comparison. For full explanations, see text. **2.** The pitted appearance of the ectodermal surface of an early hybrid gastrula; **3.** The furrow encircling the hybrid egg and the narrow depression on the dorsal side representing the neural groove; **4.** *Top:* normal appearance of the tail-bud stage (stage 17) in a control embryo; *Bottom:* hybrid embryo with extreme reduction of head, fused oral suckers projecting from head, and the ventral abdominal bulge; **5.** *Top:* heart beat stage (stage 19) in a control embryo; *Bottom:* shrivelled appearance of hybrid embryo showing abbreviated head,

only a few developmental irregularities (total average of nine percent for four groups of embryos) were noted in the Mexican embryos. In contrast, the Wisconsin embryos developed only as far as the neurula stage. Moreover, development was normal in the Mexican embryos at 27.5°C, whereas 85 percent (390 of a total of 460 eggs) of the Wisconsin tadpoles were distorted.

At the low temperature extreme, adequate temperature control was not available. However, some indication of the differential effects of low temperature on the embryos was obtained by placing the developing eggs in a refrigerator which fluctuated from 6°C to 9°C. Four groups of Mexican eggs (total of 392 eggs) failed to cleave and 436 Wisconsin eggs developed normally up to stage 17 (300 hours), at which time the experiment was terminated. It appears that the embryos of *R. pipiens* from Wisconsin behave like those of other northerly distributed amphibians in being able to tolerate low temperatures.

In all probability, the differences in rate of development and temperature tolerance of Mexican and Wisconsin eggs represent adjustments that adapt the eggs to their respective environments. However, data on prevailing environmental conditions, particularly temperatures of their breeding waters, are lacking. Also, it seems reasonable to suspect that the improper interadjustments of morphogenetic movements observed in hybrid development (discussed below) are attributable, at least in part, to conflicting modes of action of temperature-related processes.

Reciprocal artificial hybridizations.—The procedure in artificial hybridization consisted of fertilizing the eggs of one female from a particular locality in two batches: the first with the sperm of a male derived from the same locality ("control"), and the second with the sperm of a male from a different locality ("hybrid"). Eight hybrid crosses were conducted, four of which involved a Mexican *pipiens* egg and a Wisconsin *pipiens* sperm each with controls ("Type A" cross); the others were reciprocal crosses each with controls ("Type B" cross). The hybrid embryos from the two types of crosses were

---

ventral abdominal bulge, and the curved tail (the confining inner jelly membrane is not shown); **6.** *Top:* gill circulation stage (stage 20) in a control embryo which has hatched from the jelly membranes; *Bottom:* hybrid embryo showing little progress made over previous stage (fig. 5); the hybrid embryo is still trapped within the inner jelly membrane, but this is not shown in the illustration; **7.** *Top:* gill circulation stage (stage 20) in a control embryo; *Bottom:* an exceptional hybrid embryo which has hatched, showing the wrinkled blastocoele roof in the ventral abdominal region and the microcephalic condition with the downward projecting fused oral suckers; **8.** *Top:* tail fin circulation stage (stage 22) in a control embryo; *Bottom:* a surviving hybrid embryo in which considerable reorganization has taken place: the ventral abdominal bulge has disappeared and the head tends toward a normal condition; however, mouth and eye formations are atypical.

characterized by retarded developmental rates and extensive structural abnormalities. Within each type of cross the results were essentially similar; thus only a single cross of each type will be described in detail.

Type A, Cross 1:

La Union, Mexico ♀ X Oshkosh, Wisconsin ♂
La Union, Mexico ♀ X La Union, Mexico ♂ (Control)
Conducted at 18.9°C.

The rate of development in the early cleavage stages was maternal and the cleavage furrows were normal. The first indication of hybrid abnormality appeared during gastrulation. The surface of the presumptive ectoderm area overlying the blastocoele became wrinkled and presented a pitted appearance (fig. 2). During the closure of the blastopore and the subsequent formation of the neural folds, the series of pits arranged themselves in the form of a groove or furrow encircling the ventral portion of the egg (fig. 3). The groove marked externally the floor of the blastocoele. This was determined by puncturing a few eggs with a needle slightly below the groove. Blastocoele fluid escaped and yolk cells occupied the internal area at the level delimited externally by the groove. Thus the blastocoele failed to become completely obliterated during the gastrular movements. The persistent blastocoele later assumed the shape of a bulge in the ventral abdominal region of the developing hybrid embryos. The neural folds that formed in the hybrid embryos were narrower and closer together than in the control embryos. This condition foreshadowed the future reduction of the head. Figure 4 shows the extreme reduction and abnormalities of the anterior region of hybrid embryos at the tail bud stage. The oral suckers were greatly reduced in size and fused; the olfactory pits were absent or, if present, approached one another toward the mid-line; the stomadeal groove was absent; the gill plate showed no visible differentiation into arches; and the ventral abdominal bulge filled with blastocoele fluid was prominent. By late stage 19, the control embryos had already hatched (fig. 5). The majority of the hybrid embryos remained curled within the inner jelly membrane and failed to hatch. The structural abnormalities in the hybrid embryos were pronounced. The ventral abdominal bulge remained relatively large; the fused oral suckers projected downward; no stomadeal pit was present; and the gill plates remained undifferentiated and drawn close to the head. The hybrid embryos appeared arrested at this time. When the controls reached stage 20 (gill circulation), no advances were made by the hybrid embryos over the prior stage (fig. 6). Most of them cytolyzed within the inner jelly mass. However, some of the hybrids hatched. In those hatching, either the bulge in the ventral ectoderm became wrinkled and cytolysis ensued, or, in a very small percent, the bulge became reduced in size (fig. 7). Of the latter a few continued development into stage 22 (fig. 8). In these surviving hybrid embryos, the small fused suckers began to disappear, but the development of the mouth structures and eyes were much delayed and small.

These hybrids were transferred to a balanced aquarium, but all failed to live. Death was associated with reduced heads, abnormal eyes and atypical mouthparts, as control embryos placed in the same tank at the same time continued developing.

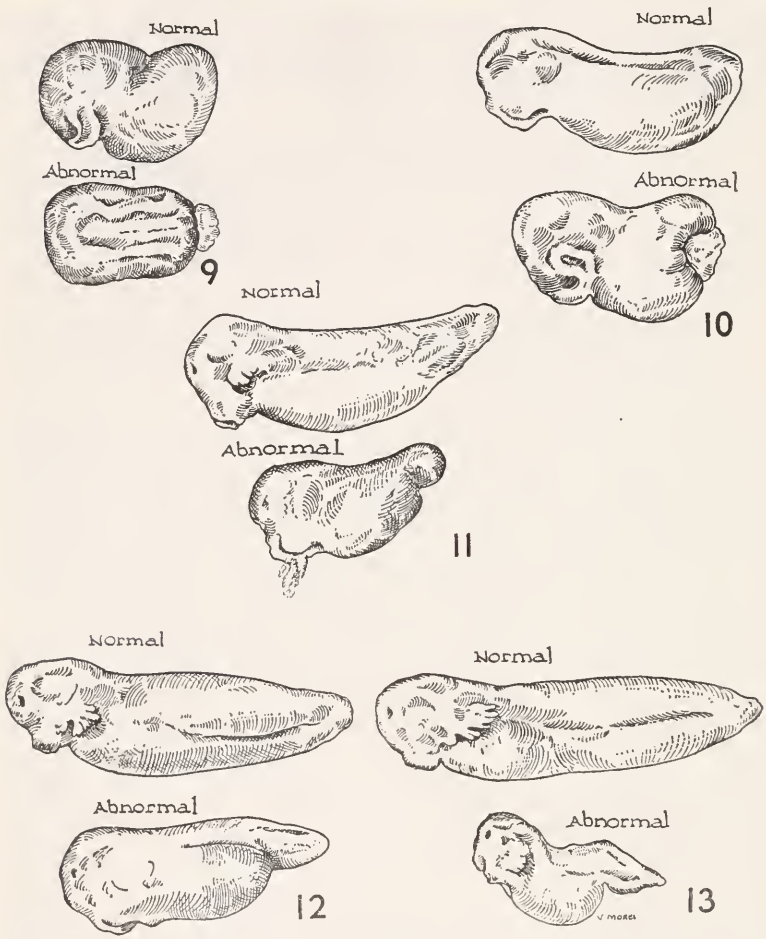
The hybrid abnormalities described above were also noticed in the other crosses of Mexican ♀ X Wisconsin ♂ ("Type A"). Hybrid embryos of this type of cross characteristically exhibited reduced heads with fused suckers and fused olfactory pits. In each of the four "Type A" crosses conducted, all hybrid embryos died.

Type B, Cross 1:

Oshkosh, Wisconsin ♀ X 29 km. e. El Mante, Mexico ♂
Oshkosh, Wisconsin ♀ X Oshkosh, Wisconsin ♂ (Control)
Conducted at 18.9°C.

The defects observed in these hybrid embryos were different, in fact almost opposite to those described in the "Type A" cross. Many embryos failed to recover from the effects of abnormal gastrulation. The disintegrating gastrulae exhibited open blastopores with extruding yolk plugs. However, a fair percent formed neural plates though the blastopore remained open (fig. 9). The neural folds that developed in the anterior end of the hybrid embryos were more divergent than encountered in the controls. This foreshadowed the enlarged head that appeared in later development. As shown in figure 9, the hybrid embryos were markedly retarded in development (the controls were in late stage 16). During later development (fig. 10), the hybrid embryos showed open blastopores of varied sizes. An atypical tail bud developed from the median dorsal lip of the open blastopore. Characteristic defects, other than the persistent yolk plug and shortened tail, were the enormous head, the abbreviated body form, and the unusually immense, widely-separated oral suckers. When the controls reached stage 19 (fig. 11), the surviving hybrid embryos were considerably retarded. An unnatural mucus mass filled the space between the huge oral suckers. As the controls progressed to stage 20 (fig. 12) the hybrids showed little developmental advance. The oral suckers remained large and divergent, and the blastopore beneath a shortened tail remained open in most embryos. By the time the controls were in stage 22 (fig. 13) all the hybrid embryos died. Cytolysis appeared to begin first in the yolk cells of the exposed yolk plug. The cytolyzing embryos showed enlarged heads, immense oral suckers, curved tails, and poorly differentiated gill plates. A few, prior to death, showed the earliest beginnings of external gills, but corpuscles were never observed coursing through them.

The hybrid embryos in the three other "Type B" crosses were characterized by the same kind and intensity of abnormalities. Not a single functional tadpole was obtained in all the crosses involving Wisconsin eggs and Mexican sperm.



Figures 9-13. Development of hybrid embryos from the cross Oshkosh, Wisconsin ♀ X Tampico, Mexico ♂. Control embryos (Oshkosh, Wisconsin ♀ X Oshkosh, Wisconsin ♂) are shown in all figures for comparison. For full explanation, see text. **9.** *Top:* a control embryo approaching tail bud stage (stage 17); *Bottom:* retarded hybrid embryo in medullary plate stage (stage 13), showing the open blastopore with the large, extruding yolk plug; **10.** *Top:* tail bud stage (stage 17) in a control embryo; *Bottom:* hybrid embryo showing the exposed yolk plug and the large, divergent oral suckers; **11.** *Top:* heart beat stage (stage 19) in a control embryo; *Bottom:* hybrid embryo with an enlarged head, stubby tail, and a thick mucus mass projecting from the overactive oral suckers; **12.** *Top:* gill circulation stage (stage 20) in a control embryo; *Bottom:* a hybrid embryo arrested in development; abnormal in those respects previously noted; **13.** *Top:* tail fin circulation stage (stage 22) in a control embryo; *Bottom:* appearance of a hybrid embryo just prior to cytolysis; note the enlarged head, shortened body form, and poorly differentiated tail.

Discussion

It is clear that isolation through hybrid inviability has reached a high intensity between Oshkosh, Wisconsin *Rana pipiens* and those from the area of Tamaulipas, Mexico. Moore (1947) demonstrated a similar high degree of incompatibility between Alburg, Vermont and eastern Mexico meadow frogs. It may have been argued that the observed hybrid abnormalities were due to certain characteristics unique only to Vermont meadow frogs among northern *pipiens* or to an equally peculiar property of those meadow frogs from the particular Mexican localities studied by Moore. Similar results in this investigation utilizing *pipiens* from another northern locality and different Mexican localities suggest the likelihood that all northern meadow frogs could not cross with their southerly-distributed lowland relatives in Mexico. The geographically extreme members of the species range have built up different adaptive gene complexes to the extent that they are incapable of producing viable hybrids in the laboratory.

It must be admitted that the probability of a Wisconsin meadow frog crossing with a Mexican frog in nature is extremely remote. Yet it is just this point which emphasizes the fact that incipient isolating mechanisms do not develop initially for the effect itself, but are simply the inevitable consequence of two populations accumulating sufficient adaptive genetic differences during a period of geographical separation. Muller (1942) was among the first to favor this concept that isolating mechanisms arise as a by-product of genetic divergence of allopatric populations. The genetic changes which arise to better adapt one population to particular environmental factors may also be instrumental in isolating to varied degrees that population from other populations which may possess different adaptive, incidentally isolating, pleiotropic alleles. In our case, genetic differentiation of the allopatric *pipiens* populations has proceeded to such a marked degree that isolation is almost complete. Presumably the genes or gene complex governing different temperature requirements of the two types of eggs also have very strong isolating effects. If the Wisconsin and Mexican *pipiens* were ever to meet in nature, natural selection would probably reinforce the isolation thru hybrid inviability by additional mechanisms which would guard against the production of hybrids and thus prevent the wastage of reproductive energy. Recently, Koopman (1950) has demonstrated experimentally an increase in the amount of reproductive isolation between two species of *Drosophila* as a result of continual artificial selection.

Of embryological interest is the demonstration that the results of hybridization between the two geographically extreme groups are very dissimilar in the reciprocal crosses. The gastrulation process is differentially affected in each type of hybrid development. In

the cross Mexican *pipiens* ♀ X Wisconsin *pipiens* ♂, the invaginative phase (internal rearrangement of groups of cells) of gastrulation is most seriously hampered, whereas in the reciprocal cross the progress of the blastopore lips over the yolk (epiboly of gastrulation) appears to be most disturbed. These early defects in the gastrular movements are responsible for the major subsequent abnormal form changes in each type of cross. In the cross Mexican *pipiens* ♀ X Wisconsin *pipiens* ♂, restriction of internal yolk movement results in the failure of the blastocoele to be completely obliterated. As the persistent blastocoele offers resistance to the involuting chorda-mesoderm, the latter is abnormally disposed in the anterior head region and this probably accounts for the subsequent microcephaly. In the reciprocal cross (Wisconsin *pipiens* ♀ X Mexican *pipiens* ♂), restriction of the epibolic spreading of the animal hemisphere results in a permanently open blastopore. The exposed yolk-plug later cytolyzes under the irregularly curved, shortened tail. Although the abnormalities in the posterior region of these hybrid embryos are traceable back to an open blastopore, the origin of macrocephaly in the anterior region is not apparent from the observations made.

As has been shown, normally fertilized eggs of Wisconsin and Mexican *pipiens* differ considerably in their rate of development. This is the most obvious physiological difference between the two eggs, and one may be tempted to propose that an asynchronous developmental rate in the hybrid egg is the factor initially responsible for the observed abnormalities. It is hazardous, however, to suggest that this may be the actual causative mechanism. The hybridization experiments were conducted at 18.9°C and 21.1°C; temperatures at which the developmental rates of Wisconsin and Mexican eggs differ. It would have proved interesting to run the hybridization experiments at 19.8°C, a temperature at which (interpolated from figure 1) the rates of development are the same. An insufficiency of frogs from Tamaulipas, Mexico frustrated efforts along this line, but it appears likely that the same types and intensity of developmental abnormalities would have been encountered if the reciprocal crosses were conducted at 19.8°C. The causative mechanism thus remains problematic. Others have attributed heterogenic hybrid abnormalities to a variety of factors: altered activity or inactivation of the sperm nucleus, disturbance of the nucleo-plasmic ratio, competition of enzymes for limited substrates, etc.

Successful interpretation of our case and others is further complicated by the demonstration that modifications in amphibian development produced by direct action of a variety of chemical and physical agents simulate in many ways inhibitions in hybrid development (see Child, 1941).

Summary

1. The geographically extreme members of *Rana pipiens* from Tamaulipas, Mexico, and Oshkosh, Wisconsin, are characterized by different embryonic rates of development and embryonic temperature tolerances, which may represent differential adaptations to the water temperatures in nature to which the eggs of each group are subjected.

2. Experimental hybrids between Wisconsin and Mexican meadow frogs show such marked embryonic abnormalities that none would survive if the respective parental populations were to become sympatric and hybridize in nature. The evolutionary tenet that the earliest indication of reproductive isolation appears as a by-product of the genetic divergence of allopatric populations is supported.

3. The types of embryonic abnormalities in the reciprocal hybrids follow definite patterns. Hybrid embryos derived from the cross Mexican ♀ X Wisconsin ♂ exhibit persistent blastocoeles, microcephaly, fused suckers and olfactory pits, reduced mouthparts, and atypical eyes. Hybrid embryos from the reverse cross, Wisconsin ♀ X Mexican ♂, possess enlarged yolk plugs, macrocephaly, overdeveloped suckers, shortened bodies, and curved tails.

References Cited

Child, C. M. 1941. *Patterns and Problems of Development.* University of Chicago Press, Chicago, Illinois.

Koopman, K. F. 1950. Natural selection for reproductive isolation between *Drosophila pseudoobscura* and *Drosophila persimilis. Evol.*, 4: 135-148.

Moore, J. A. 1946. Incipient intraspecific isolating mechanisms in *Rana pipiens. Genetics*, 31: 304-326.

———— 1947. Hybridization between *Rana pipiens* from Vermont and eastern Mexico. *Proc. Nat. Acad. Sci.*, 33: 72-75.

———— 1949a. Patterns of evolution in the genus *Rana. In:* Jepsen, G. L., G. G. Simpson, and E. Mayr (eds.), *Genetics, Paleontology, and Evolution.* Princeton University Press, Princeton, New Jersey.

———— 1949b. Geographic variation of adaptive characters in *Rana pipiens* Schreber. *Evol.*, 3: 1-24.

Muller, H. J. 1942. Isolating mechanisms, evolution and temperature. *Biol. Symp.*, 6: 71-125.

Pollister, A. W. and J. A. Moore. 1937. Tables for the normal development of *Rana sylvatica. Anat. Rec.*, 68: 489-496.

Volpe, E P. 1952. Physiological evidence for natural hybridization of *Bufo americanus* and *Bufo fowleri. Evol.*, 6: 393-406.

———— 1953. Embryonic temperature adaptations and relationships in toads. *Physiol. Zool.*, 26: 344-354.

NA-N[ew Orleans]

TULANE STUDIES IN ZOOLOGY

Volume 1, Number 10 April 30, 1954

THE BUTTERFLIES AND SKIPPERS OF LOUISIANA

EDWARD NELSON LAMBREMONT,
NEW ORLEANS.

MUS. COMP. ZOOL.
LIBRARY
MAY 11 1954
HARVARD
UNIVERSITY

TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico and the Caribbean Sea. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

WILLIAM T. M. FORBES, Professor of Entomology, Cornell University, Ithaca, New York.

AUSTIN H. CLARK, Curator of Echinoderms, United States National Museum, Washington, D. C.

RALPH L. CHERMOCK, Associate Professor of Biology, University of Alabama, University, Alabama.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

When citing this series authors are requested to use the following abbreviations: *Tulane Stud. Zool.*

Price for this number: $0.60.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University,
New Orleans, U. S. A.

Assistants to the Editor:
Carol L. Freret
Robert E. Gordon

LIBRARY
MAY 11 1954
HARVARD UNIVERSITY

THE BUTTERFLIES AND SKIPPERS OF LOUISIANA[1]

EDWARD NELSON LAMBREMONT,
New Orleans

Prior to the summer of 1948 when a project to survey the butterflies and skippers of Louisiana was started there existed only scattered records and four parish lists. The oldest of these was published as a catalog of the Lepidoptera of New Orleans and its vicinity by Ludwig von Reizenstein in 1863. As originally published the records of von Reizenstein could not have been included in this paper because the basis of von Reizenstein's determination of species was unknown. Twenty-six of the species, however, were checked against Morris (1862) and are included with the other records. Six species, as yet unidentifiable, are listed for general interest in Table 1.

Kopman (1903) published a popular account of the butterflies of Louisiana in the *New Orleans Times Democrat.* Of the 24 species recorded only three have definite localities noted and are included herein. Hine (1904, 1906) listed the Lepidoptera of Cameron parish in the southwestern corner of the state, including valid records for 15 species, and Montgomery (1932) listed 15 species from Madison and Tensas parishes in the northeastern corner. Glick (1939) listed eight species from Madison parish. All other publications deal with only a few species.

From these publications a small, highly localized list may be compiled consisting of 43 species, including four type localities, in the state.

The best and most recent local study was published since the initiation of this survey. It consists of collections and notes made by Jung (1950) within Orleans, Jefferson, Plaquemines, and St. Bernard parishes. Thirty-seven species of butterflies and skippers are recorded, 17 of which had not been reported from the state previously.

Taking Jung's paper (1950) into consideration the state list numbered 60 species and subspecies. The present survey, concluded in March 1951, adds 38 previously unrecorded species and subspecies, bringing the total to 98 (Table 2). This is by no means to be considered all the species that should be found, for many that are known to occur in nearby areas have not been taken within Louisiana's borders. The rich fauna of Texas and Mexico undoubtedly overlaps part of Louisiana, particularly the southwest, and many of the Texas-Mexican forms have been taken short distances from the Louisiana-Texas line. In all probability the number of species would have reached about 140 if the survey had been continued. Completion of the survey would require considerable collecting in the state during certain seasons of the year, particularly in the spring. On the basis

[1] From a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science of the Graduate School of Tulane University.

TABLE 1.

SPECIES RECORDED BY VON REIZENSTEIN (1863) WHICH WERE UNIDENTIFIABLE. NOTES ARE PRESENTED EXACTLY AS THEY APPEAR IN THE ORIGINAL; COMMENTS BY THE WRITER ARE IN PARENTHESES.

Goniopteryx Eclipsis.

Xanthidia Sylvatica, MSS Rare.

Heliconia diaphona Drur. Rare Western Lake Shore. (Probably *H. charitonius*)

Euptoieta hegesia? Cram. City Park. On Passiflorae. (Probably *E. claudia*)

Apatura myops, MSS. On elm trees.

Thecla io, MSS. City Park, rare. On camomilla.

of their overall distributional patterns approximately 40 additional species may be anticipated to occur in Louisiana. These are listed in Table 3, but otherwise are not mentioned in this paper.

AREA STUDIED

Including islands in the Gulf of Mexico the total area of Louisiana is 48,506 square miles, of which 3,097 square miles are water surface (1,060 square miles of landlocked lakes). The entire state is within Merriam's Austroriparian life zone; the northern portion within the Carolinian area, and the southern portion in a semi-tropical region called the Gulf Strip.

Viosca (1933) divided Louisiana into four main physiographic areas which are illustrated in figure 1. Each of these supports a characteristic flora. As will be noted later the distribution of certain butterflies and skippers is correlated with these areas to some extent. In addition to the natural vegetation there are many man-made communities which tend to obscure the relation between natural vegetation and physiographic areas. Such man-made disturbance communities are: pine-hardwood, scrub-oak grassland, successional changes on abandoned farmlands, and undeveloped agricultural land-reclamation projects. These man-made disturbance areas support many small flowering plants, both natural and horticultural, which are attractive to butterflies and skippers.

With the exception of the coastal ridge and delta division all major physiographic regions of Louisiana were sampled intensively during the two-and-one-half year term of this survey. Those places within short distances from New Orleans were concentrated upon, but three major trips totalling more than 50 days in the field were taken to collect in the northern uplands. The accompanying map (fig. 2) shows the distribution of collections. To facilitate travel and increase the range only a few areas were sampled over any length of time. These include the Sabine parish area; Caddo and neighboring

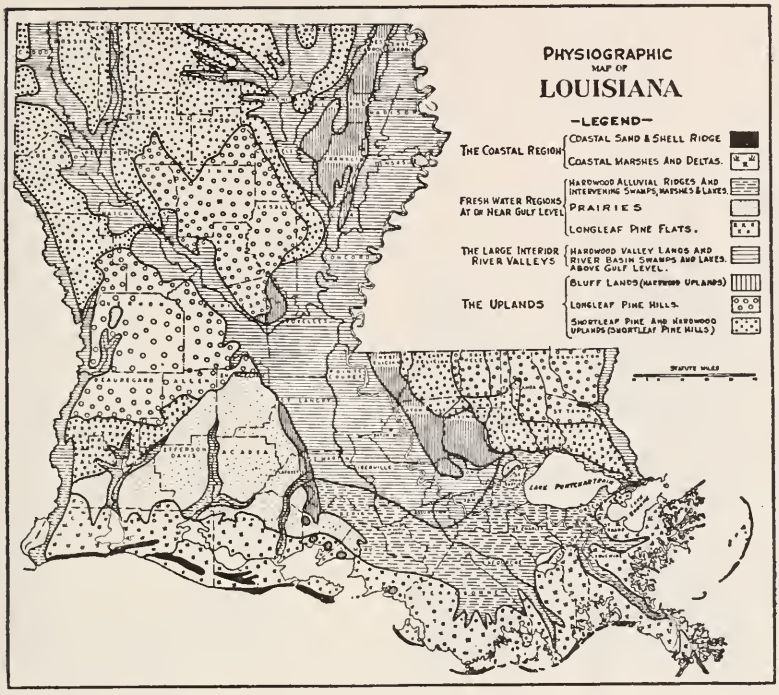


Figure 1. Physiographic map of Louisiana from Viosca (1933). Reprinted by permission of the copyright owner.

parishes; Lincoln-Jackson-Union parish area; Ouachita-Morehouse and parishes east; Concordia parish and surrounding area; Allen parish and all parishes east to the Mississippi river, excluding West Baton Rouge; the Florida parishes; and New Orleans and vicinity.

Most of the collections were made during the summer months. The only heavily collected sections during other times of the year were the Jackson-Lincoln-Union area in the spring, Allen parish and all parishes east to the Mississippi river in the fall, and the Florida parishes and New Orleans and vicinity throughout the year.

The majority of the butterflies and skippers were taken by the author from June 1948 to April 1951; records previous to this time were contributed by other members of the Tulane University zoology staff.

Systematic Treatment

Each species is considered individually. Each such treatment includes a summary of observations and Louisiana distribution records. The arrangement of species follows Klots (1951).

Where specific data are required the records are listed alphabetically by parish, each including the following: locality (within five miles

TABLE 2
LIST OF LOUISIANA SPECIES CONTRASTING PREVIOUSLY REPORTED MATERIAL WITH THE NEW RECORDS ADDED HEREIN.

From Literature	New Records
	SATYRIDAE
Lethe portlandia portlandia (Fabricius)	Euptychia gemma gemma (Hübner)
Euptychia hermes sosybius (Fabricius)	Euptychia areolata areolata (J. E. Smith)
	Euptychia cymela cymela (Cramer)
	Cercyonis pegala pegala (Fabricius)
	Cercyonis pegala alope (Fabricius)
	DANAIDAE
Danaus plexippus plexippus (Linné)	
Danaus plexippus melanippe (Linné)	
Danaus gilippus berenice (Cramer)	
	NYMPHALIDAE
Heliconius charitonius tuckeri Comstock & Brown	Dryas julia delila (Fabricius)
Agraulis vanillae nigrior Michener	Speyeria cybele (Fabricius)
Euptoieta claudia claudia (Cramer)	Melitaea nycteis nycteis Doubleday
Phyciodes gorgone (Hübner)	Nymphalis antiopa antiopa (Linné)
Phyciodes tharos tharos (Drury)	
Polygonia interrogationis (Fabricius)	
Vanessa atalanta atalanta (Linné)	
Vanessa cardui cardui (Linné)	
Vanessa virginensis (Drury)	
Precis evarete coenia (Hübner)	
Limenitis archippus watsoni (dos Passos)	
Limenitis arthemis astyanax (Fabricius)	
Anaea andria (Scudder)	
Asterocampa clyton clyton (Boisduval & LeConte)	
Asterocampa celtis celtis (Boisduval & LeConte)	
Asterocampa celtis alicia (Edwards)	
	LIBYTHEIDAE
Libytheana bachmannii bachmannii (Kirtland)	
	RIODINIDAE
Calephelis virginiensis (Guerin)	
	LYCAENIDAE
Atlides halesus halesus (Cramer)	Strymon ontario autolycus (Edwards)
Strymon cecrops (Fabricius)	Strymon liparops liparops (Boisduval & LeConte)
Strymon melinus melinus (Hübner)	Hemiargus isolus (Reakirt)
Incisalia irus (?) (Godart)	Celastrina argiolus pseudargiolus (Boisduval & LeConte)
Feniseca tarquinius tarquinius (Fabricius)	
Everes comyntas comyntas (Godart)	

Papilio polyxenes asterias Stoll
Papilio cresphontes cresphontes Cramer
Papilio glaucus glaucus (Linné)
Papilio troilus troilus Linné
Papilio palamedes palamedes Drury
Graphium marcellus marcellus (Cramer)
Battus polydamus lucayus (Rothschild & Jordan)
Battus philenor philenor (Linné)

Colias eurytheme eurytheme Boisduval
Zerene cesonia (Stoll)
Phoebis sennae sennae (Linné)
Phoebis sennae eubule (Linné)
Eurema nicippe nicippe (Cramer)
Euremia lisa (Boisduval & LeConte)
Nathalis iole Boisduval
Pieris rapae (Linné)
Pieris protodice protodice Boisduval & LeConte
Ascia monuste phileta (Fabricius)

Epargyreus clarus (Cramer)
Urbanus proteus (Linné)
Pyrgus communis communis (Grote)
Celotes nessus (Edwards)
Erynnis horatius (Scudder & Burgess)
Ancyloxypha numitor (Fabricius)
Hesperia leonardus stallingsi H. A. Freeman
Hylephila phyleus (Drury)
Poanes viator (Edwards)
Oligoria maculata (Edwards)
Lerema accius (J. E. Smith)
Lerodea eufala (Edwards)
Calpodes ethlius (Stoll)
Panoquina panoquin (Scudder)

Papilionidae

Papilio troilus ilioneus J. E. Smith

Pieridae

Anthrocharis genutia genutia (Fabricius)
Colias philodice philodice (Latrielle)
Phoebis philea (Linné)
Phoebis agarithe maxima (Neumoegen)
Eurema daira daira (Latrielle)

Hesperiidae

Achalarus lyciades (Geyer)
Thorybes bathyllus (J. E. Smith)
Thorybes confusis Bell
Pholisora hayhurstii (Edwards)
Erynnis juvenalis (Fabricuis)
Copaeodes minima (Edwards)
Atalopedes campestris (Boisduval)
Polites manataaqua manataaqua (Scudder)
Polites themistocles (Latreille)
Polites vibex brettus (Boisduval & LeConte)
Wallengrenia otho otho (J. E. Smith)
Atrytone arogos arogos (Boisduval & LeConte)
Atrytone dukesi Lindsey
Atrytone ruricola metacomet (Harris)
Amblyscirtes vialis (Edwards)
Amblyscirtes textor (Hübner)
Lerodea l'herminieri (Latreille)
Panoquina ocola (Edwards)

TABLE 3

SPECIES EXPECTED TO OCCUR IN LOUISIANA BUT NOT YET RECORDED

	SATYRIDAE
Lethe creola (Skinner)	Lethe eurydice (Johannson)
	NYMPHALIDAE
Melitaea ismeria (Boisduval & LeConte)	Asterocampa clyton flora (Edwards)
Phyciodes texana seminole (Edwards)	
	LYCAENIDAE
Strymon m-album (Boisduval & LeConte)	Mitoura gryneus (Hübner)
Strymon titus mopsus (Hübner)	Incisalia niphon niphon (Hübner)
Strymon favonius (J. E. Smith)	Hemiargus ceranus antibastus (Hübner)
Strymon ontario ontario (Edwards)	Brephidium pseudofea (Morrison)
Strymon falacer (Godart)	
	PIERIDAE
Eurema mexicana (Boisduval)	
	HESPERIIDAE
Thorybes pylades Scudder	Polites peckius (Kirby)
Pholisora catullus (Fabricius)	Poanes yehl (Skinner)
Erynnis icelus (Scudder & Burgess)	Problema byssus (Edwards)
Erynnis brizo brizo (Boisduval & LeConte)	Atrytone logan logan (Edwards)
Erynnis martialis (Scudder)	Atrytone alabamae Lindsey
Erynnis baptisiae Forbes	Atrytone dion (Edwards)
Erynnis zarucco (Lucas)	Atrytonopsis hianna (Scudder)
Hesperia sassacus (Harris)	Amblyscirtes alternata (Grote & Robinson)
Hesperia meta (Scudder)	Amblyscirtes belli H. A. Freeman
Hesperia attalus (Edwards)	Lerodea neamathla Skinner & Williams
Hesperia meskei (Edwards)	Megathymus yuccae Boisduval & LeConte
Polites verna (Edwards)	Megathymus cofaqui Strecker

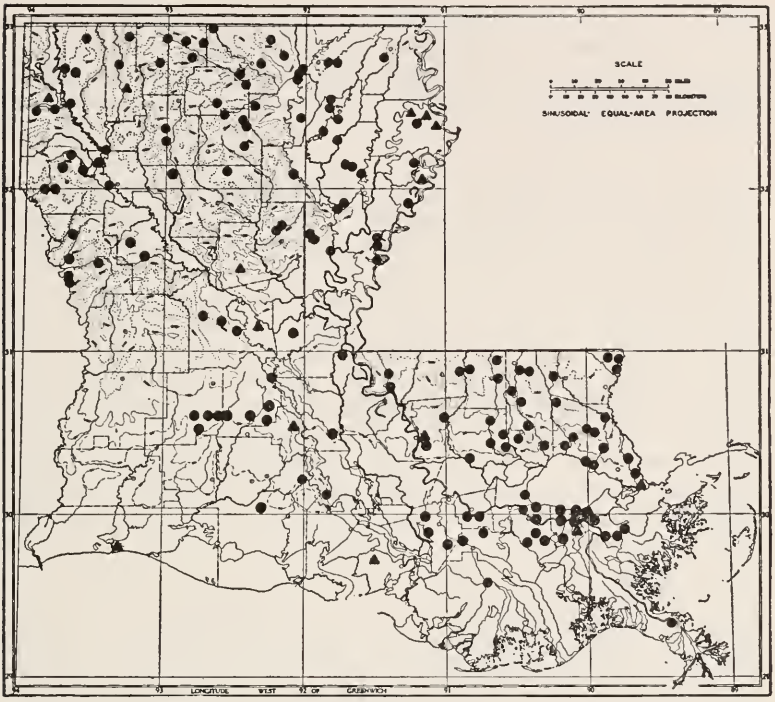


Figure 2. Map showing distribution of localities from which material was examined, or previously recorded; triangles = localities from the literature; dots = localities from the present survey.

of nearest Post Office), date of collection, number and sex of specimens, and institutional location of specimens in parentheses. Unless otherwise specified all specimens are in the Tulane collection. Abbreviations of the institutions are: LPI = Louisiana Polytechnic Institute, Ruston; LSM = Louisiana State Museum, New Orleans; SLI = Southwestern Louisiana Institute, Lafayette; TU = Tulane University ("P" series are collections prior to 1947 with sparse data; lot numbers P-955 through P-1101 consist of the James M. McArthur Collection).

Superfamily PAPILIONOIDEA, The Butterflies
Family SATYRIDAE

LETHE PORTLANDIA PORTLANDIA (FABRICIUS), the Pearly Eye.—The writer has not taken this species; however, Skinner (1897) described a specimen captured in Louisiana as *L. creola.* Dr. Austin H. Clark informed the writer (in correspondence) that this supposed *creola* is actually *portlandia.* Skinner's record is: *St. Landry:* Opelousas, VII-3-1897.

EUPTYCHIA CYMELA CYMELA (CRAMER).—The Little Wood-satyr

is rather common in Louisiana during the spring and early summer; earliest and latest dates recorded are April 1, 1950 (8 ♂♂) and June 24, 1950 (1 ♀). It is most often seen in woody places, particularly in pinelands, and most of the specimens have been taken in the upland pine areas of the state.

E. cymela cymela has not been recorded from Louisiana previously. Twenty-four specimens (12 ♂♂, 12 ♀♀) have been examined from 14 localities in the following parishes: Catahoula, Jackson, Lafayette (SLI), LaSalle, Lincoln, Morehouse, Ouachita, St. Tammany, Union and Washington.

EUPTYCHIA HERMES SOSYBIUS (FABRICIUS).—The Carolinian Satyr is undoubtedly the most abundant satyrid; it is probably rivaled by only two other species, *Eurema lisa* and *Phyciodes tharos,* in being the most common butterfly in Louisiana. This satyrid is particularly abundant in woody areas, especially in pinelands and oak forests, where it remains in quiet shaded spots rather than in the sunny habitats of most other butterflies. This subspecies flies the year round; specimens have been collected in all months except January and August. Earliest and latest dates are February 10, 1943 (1 ♂) and December 25, 1949 (1 ♀).

One hundred and nine specimens (64 ♂♂, 45 ♀♀) have been examined from 51 localities in the following parishes: Allen, Assumption, Catahoula, Claiborne, Evangeline, East Feliciana, Jackson, Jefferson, Lafayette (SLI), Lincoln, Livingston, Morehouse, Orleans, Ouachita, Pointe Coupee, Richland, Sabine, St. Helena, St. Landry, St. Tammany, Tangipahoa, Union, Washington, West Carroll and West Feliciana. Previously it had been recorded from Cameron (Hine, 1906) and Orleans parishes (von Reizenstein, 1863).

EUPTYCHIA AREOLATA AREOLATA (J. E. SMITH), the Georgia Satyr.—All specimens were collected in the longleaf pine flats north of Lake Pontchartrain. Supposedly the species ranges as far west as Texas, but the results of this survey indicate it must be rare west of the Mississippi river, although it localizes and can be overlooked. It resembles *E. hermes* in habits and flight by keeping close to the ground.

E. areolata areolata has not been recorded from Louisiana previously. The 31 specimens (15 ♂♂, 16 ♀♀), examined were collected from the following localities: *Livingston*: Springville, IX-6-50 (TU 2184); *St. Tammany*: St. Tammany, V-12-49 (TU 1219); Hickory, V-12-50, VI-2-50, VI-29-50, IX-30-50 (TU 1948, 1973, 2000, 2198); Covington, IX-5-50, IX-8-50 (TU 2180, 2197); Folsom, IX-7-50 (TU 2187); Talisheek, IX-13-50 (TU 2200); *Tangipahoa*: Ponchatoula, IX-6-50 (TU 2182); Robert, IX-6-50 (TU 2185); *Washington:* Angie, VI-5-50 (TU 2034).

EUPTYCHIA GEMMA GEMMA (HUBNER), the Jeweled Brown.—This beautiful woodland butterfly resembles *E. hermes* closely in habits, but it is considerably less common for only three specimens (all females) have been taken in Louisiana. From the writer's expe-

rience the species occurs in pinelands, and several which eluded capture were seen in the longleaf pine flats of St. Tammany parish.

This species has not been recorded from Louisiana previously. The three records are: *Richland*: Girard, VI-27-50 (TU 2081); *St. Tammany*: Mandeville, X-26-49 (TU 1599); *Tangipahoa*: Tangipahoa, IX-7-50 (TU 2192).

CERCYONIS PEGALA PEGALA (FABRICIUS).—The Southern Woodnymph probably has a better protective coloration than any other butterfly except its allied subspecies, *C. pegala alope*. The insect usually may be found sitting on the sides of pine trees, and unless disturbed it is often mistaken for a loose piece of bark. The undersides of the wings are colored in such a way that they blend with the surroundings so well that one must "beat" the trees with a stick to flush them from hiding. When disturbed the butterfly quickly flies a short distance to another tree, and the same procedure must be repeated. To add to this collecting difficulty they are exceptionally hard to capture in flight. Only a few have been collected in Louisiana, perhaps because of their deceptiveness.

C. pegala pegala has not been recorded from Louisiana previously. The three records are: *St. Tammany*: Covington, IX-8-50, 1 ♂ (TU 2197); Hickory, IX-13-50, 1 ♀ (TU 2198); *Tangipahoa*: Amite, IX-7-50, 1 ♀ (TU 2195).

CERCYONIS PEGALA ALOPE (FABRICIUS), the Common Woodnymph.—In the past, authors have treated this subspecies as a separate species along with other forms of *C. pegala*. More recently some have chosen to combine all as one large clinal species. Until the *pegala-alope* complex is understood fully the writer prefers to consider them as separate subspecies. The observations given for typical *pegala* are much the same as those for *alope*.

C. pegala alope has not been recorded from Louisiana previously. The only record is: *LaSalle*: Summerville, VI-12-50, 1 ♂ (TU 2048).

Family DANAIDAE

DANAUS PLEXIPPUS PLEXIPPUS (LINNÉ).—The Monarch is one of the most interesting butterflies of our fauna, and has attracted considerable attention because of its migrations. For many years they have been known to swarm (Saunders, 1871) and migrate.

The Louisiana collections show two annual peaks of abundance of this subspecies: one in April, and the other during October and November. Judd (1950) reported a congregation of Monarchs on the north shore of Lake Erie which occurred during the last four days of August 1949, and Saverner (1908) reported swarms in Michigan which lasted from September 4 through 15. Williams (1930) quoted Shannon in saying that one of the four main routes of migrating butterflies in North America is from Canada along Lake Ontario and Lake Erie southward. Travelling at a speed of five to seven miles per hour (Park, 1948), a swarm of monarchs leaving

Canada in late August should reach the Gulf states in about a month providing there are no high winds against them. This correlates somewhat with our recorded peak of October-November, and also with a large flight which the writer observed headed southward October 10, 1949 near New Orleans, and one noted in November 1941 by Percy Viosca (newspaper article).

Originally this insect was more or less confined to North America, but with time it has spread throughout the islands of the Atlantic, and to most of the Pacific islands, including New Zealand and Australia (Williams, 1930, 1937).

Forty-five specimens have been examined (27 ♂♂, 18 ♀♀) and hundreds more have been observed in migratory flight. Collections have been made throughout the year, except January and February; earliest and latest dates are March 18, 1950 (1 ♂) and December 15, 1949 (1 ♂). The monarch has been recorded from 24 localities in the following parishes: Avoyelles (SLI), Franklin, Jefferson, Lafayette (SLI), Lincoln, Livingston, Morehouse, Orleans, Ouachita, Richland, St. Bernard, St. Charles, St. Helena, St. James, St. John the Baptist, St. Landry, St. Tammany, Tangipahoa and West Feliciana. Previously the monarch had been recorded from Cameron (Hine, 1906) and Orleans parishes (von Reizenstein, 1863; Shufeldt, 1884; Jung, 1939, 1950).

DANAUS PLEXIPPUS MELANIPPE (HUBNER), the South American Monarch.—This subspecies has caused much controversy in recent years for the figure in Holland (1898; 1931 revised) given to represent *D. plexippus plexippus* is actually the subspecies *melanippe*. Although *melanippe* is not typical for most of North America it has been captured as an occasional vititor as far north as Illinois and New York (Clark, 1941).

The Louisiana record is: *Orleans:* New Orleans, VIII-8-25, 1 ♂ (TU P-967). Previously it had been recorded from St. Tammany parish by Clark (1941).

DANAUS GILIPPUS BERENICE (CRAMER).—The Queen is a rare danaid in Louisiana. The few records show that this species flies mostly during the warmer months. One female, however, was taken in March, 1950, probably because the winter of that year was very mild. Unlike the monarch this species is not migratory.

The six specimens examined were from the following localities: *Jefferson*: Metairie, VIII-7-47 (TU 92); Bridgedale, VIII-25-50 (TU 2123); *Orleans*: New Orleans, XI-26-27, VII-1-32, III-25-50 (TU P-970, P-982, 1825); *St. Tammany*: Mandeville, X-11-49 (TU 1566). Previously it had been recorded from Cameron (Hine 1906) and Orleans parishes (Jung, 1939, 1950).

Family NYMPHALIDAE

HELICONIUS CHARITONIUS TUCKERI COMSTOCK AND BROWN.—The Zebra is not common in Louisiana, but it is seen occasionally during the summer and early autumn in the southernmost parishes.

The few records from the state were obtained in August and October. Although the writer has never seen this butterfly in the field, a few of them were reported to him from the Mississippi delta region, the southern extremity of Louisiana. Comstock and Brown (1950) recorded it from Texas. The larvae feed on passion flowers.

The few records are as fellows: *Jefferson*: Mississippi river bank opposite New Orleans, X-18-1894 (Kopman, 1903); *Orleans*: New Orleans (von Reizenstein, 1863); *Terrebonne*: Houma, VIII-9-19 (LSM).

AGRAULIS VANILLAE NIGRIOR MICHENER, the Gulf Fritillary.—This is the commonest fritillary in Louisiana. During the hot summer months swarms of them may be seen hanging on blades of grass in open fields. It flies from spring to early fall; earliest and latest dates are March 22, 1950 and November 7, 1919.

The flight is exceptionally fast, and efforts at chasing this insect on the wing usually prove unsuccessful. One trick it uses in eluding capture is to fly up to about eight feet and suddenly reverse its direction. It can change its course much faster than a running man, and the writer has often found himself giving "chase" in the opposite direction from which the butterfly was traveling. However, many specimens may be taken while they are resting. According to Williams (1937) this butterfly is migratory.

The species apparently is more abundant in the southern parishes of Louisiana. Forty-seven specimens (30 ♂♂, 17 ♀♀) have been examined from 18 localities in the following parishes: Allen, Jefferson, Lafayette (SLI), Livingston, Orleans, Plaquemines, Pointe Coupee, Rapides, St. Bernard, St. Landry, St. Tammany and Terrebonne (LSM). Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863; Michener, 1947; Jung, 1950).

DRYAS JULIA DELILA (FABRICIUS), the Julia Butterfly.—McDunnough (1938) listed this species as of doubtful North American occurrence, but Holland (1931) stated that it is an occasional visitor in the extreme South. The genus is primarily a tropical one.

D. julia delila has not been recorded from Louisiana previously. The one record is: *Lafayette*: Lafayette, XI-5-41, 1 ♂ (SLI).

EUPTOIETA CLAUDIA CLAUDIA (CRAMER).—The Variegated Fritillary is very common in Louisiana from early spring throughout the summer; earliest and latest dates are March 31, 1950 (1 ♀) and October 16, 1949 (1 ♀). The larvae feed on passion flowers and violets. Several years ago, in early July, the writer's attention was called to a vacant lot in uptown New Orleans which was literally "seeded" with chrysalids of this butterfly. Previous to the time that this lot was infested there was a dense growth of passion flowers, but after the feeding of thousands of caterpillars nothing remained but bare twigs covered with chrysalids. Needless to say the emergence of adults was sensational, and a good series of pupae was collected and reared.

Within Louisiana, *E. claudia claudia* appears to be more abundant in the southern areas. Thirty-nine specimens (20 ♂♂, 19 ♀♀) have been examined from 15 localities in the following parishes: Assumption, Concordia, Evangeline, Jefferson, Lafayette (SLI), Lafourche, Orleans, Ouachita, St. Bernard, St. Landry (SLI) and St. Martin (SLI). Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863; Jung, 1950).

SPEYERIA CYBELE (FABRICIUS), the Great Spangled Fritillary.—The single Louisiana specimen was taken in the coastal area in early October, and as the species is not common to the state, perhaps it was a straggler southward during the cooler months.

S. cybele has not been recorded from the state previously. The one record is: *Lafayette*: Lafayette, X-2-31, 1 ♂ (SLI).

MELITAEA NYCTEIS NYCTEIS DOUBLEDAY, the Silvery Checkerspot.—Holland (1931) stated that *M. nycteis* ranges from Maine to western North Carolina, and westward to the Rocky Mountains. He did not say whether it comes below the latitude of North Carolina, or stays north of there. Klots (1951) also did not mention its occurrence south of the mountains of North Carolina, Missouri and Kansas. The Louisiana records may be considered southern range extensions, but since the species is not abundant in the state it appears that Louisiana is at the southern tip of its range. A single specimen was collected in the Sabine river area (near Texas), and another near the Pearl river (near Mississippi), at opposite sides of the state. Three specimens were seen at the latter location, but only one was taken. The flight is fast and erratic.

M. nycteis nycteis has not been recorded from Louisiana previously. The two records are: *Sabine*: Zwolle, VIII-2-49, 1 ♀ (TU 1381); *Washington*: Richardson, IX-7-50, 1 ♂ (TU 2188).

PHYCIODES GORGONE (HUBNER), the Gorgone Crescent-spot.—This crescent-spot, though closely allied to it, cannot begin to approach *P. tharos* in abundance. It flies from spring to early fall in sunny places, but does not seem to be restricted to any part of the state. Earliest and latest dates are March 7, 1951 (1 ♂) and October 16, 1949 (1 ♂).

Twenty-three specimens (14 ♂♂, 9♀♀) have been examined from 14 localities in the following parishes: Allen, Assumption, Bossier, DeSoto, Evangeline, Natchitoches, Pointe Coupee, Rapides, St. Charles, St. Tammany and Union. Previously it had been recorded from Cameron (Hine, 1906) and Orleans parishes (Jung, 1950).

PHYCIODES THAROS THAROS (DRURY).—The Pearly Crescent-spot is by far the most abundant butterfly in Louisiana. With the exception of the coldest days it flies throughout the year (it has been collected in all twelve months), not only in bright open fields, but in densely shaded forests as well, and is known to cluster around wet spots on the ground (Scudder, 1889). When at rest this butterfly

has the peculiar habit of slowly raising and lowering its wings. The larvae feed on plants of the family Compositae, particularly the asters.

One hundred and thirty-one specimens (74 ♂♂, 57 ♀♀) have been examined from 68 localities in the following parishes: Allen, Assumption, Catahoula, Claiborne, Concordia, DeSoto, East Baton Rouge, East Feliciana, Evangeline, Jackson, Jefferson, Lafayette (SLI), Lafourche, LaSalle, Lincoln, Livingston, Morehouse, Natchitoches, Orleans, Ouachita, Pointe Coupee, Rapides, Richland, Sabine, St. Charles, St. Helena, St. James, St. Landry, St. Tammany, Tangipahoa, Union, Washington, Webster and West Carroll. Previously it had been recorded from Madison (Montgomery, 1932) and Orleans parishes (Jung, 1950).

POLYGONIA INTERROGATIONIS (FABRICIUS), the Question Mark.—This species is exceptionally nervous and fast in flight, which perhaps accounts for the scarcity of records. In the writer's opinion each record obtained equals at least two or three uncaught butterflies, and from sight-records it appears that this species is rather abundant in Louisiana during the spring and summer months. Earliest and latest dates are March 10, 1949 (1 ♀) and October 15, 1926 (1 ♀).

This butterfly frequents open spots and forest edges. Scudder (1889) notes that it often sucks the sap flowing from wounded trees and decaying fruits, and the writer has taken adult specimens feeding on decaying fish and turtle meat. The larvae feed on a great variety of plants, particularly of the family Urticaceae.

Eighteen specimens (7 ♂♂, 11 ♀♀) have been examined from eight localities in the following parishes: Jefferson, Lafayette (SLI), Orleans, Ouachita, Sabine, Terrebonne (LSM), Washington and West Carroll. Previously it had been recorded from Orleans parish by Jung (1950).

NYMPHALIS ANTIOPA ANTIOPA (LINNÉ), the Mourning Cloak.—This beautiful butterfly is primarily a species of the northern states, appearing only occasionally in Louisiana during the late summer and fall months. It has not been recorded from the state previously.

The three records are: *Lincoln*: Ruston (LPI); *Orleans*: New Orleans, IX-25-31, 1 ♀ (TU P-977), and VIII-25-32, 1 ♀ (TU P-983).

VANESSA ATALANTA ATALANTA (LINNÉ), the Red Admiral.—This species is well-named *atalanta* for it is one of the speediest of the nymphalids. All of the specimens were caught while occupied with feeding. The larvae feed on nettles (*Urtica* spp.)

In Louisiana, *V. atalanta atalanta* is never too abundant, but it may be seen almost throughout the year, although more often during the warmer months. Earliest and latest dates are January 30, 1950 (3 ♂♂, 2 ♀♀) and October 28, 1928 (1 ♀). Jung (1950) stated that he found it to be abundant in drained swamp areas near New Orleans.

Twenty-one specimens (8 ♂♂, 13 ♀♀) have been examined from eight localities in the following parishes: Claiborne, Jefferson, Lafayette (SLI), Orleans, Ouachita, St. Tammany, Webster and West Feliciana. It had been reported previously from Orleans parish by Jung (1939, 1950).

VANESSA CARDUI CARDUI (LINNÉ), the Painted Lady.—In Louisiana this butterfly is not quite as abundant as the related species *atalanta* and *virginiensis,* the few records indicating that it flies from spring throughout the summer and autumn. Earliest and latest dates are May 3, 1924 (1 ♀) and October 18, 1949 (1 ♂).

Williams (1937) described the migrations of *cardui,* noting that in 1931 their abundance in the northern states brought help to the farmers because of the vast destruction of thistles, the food plant of their larvae. Yet in other years they do considerable damage to artichokes.

The specimens taken in the state were from open, sunny fields, and on the shrubs bordering forests. Only one was taken on thistle.

The localities are: *Caddo*: Shreveport, VIII-5-49, 1 ♀ (TU 1432); *Orleans*: New Orleans, V-3-24, 1 ♀ (TU P-957); *St. Bernard*: Shell Beach, X-18-49, 1 ♂ (TU 1595); *St. Landry*: Cortableu, X-16-49, 1 ♀ (TU 1580). Previously it had been recorded from Cameron (Hine, 1906) and Orleans parishes (von Reizenstein, 1863).

VANESSA VIRGINIENSIS (DRURY).—Hunter's Butterfly is fairly common in Louisiana through most of the year; earliest and latest dates are January 21, 1950 (3 ♂♂) and October 10, 1930 (1 ♀). Most of the specimens were taken while feeding, for like its ally, *V. atalanta,* this species is a strong flier. The larvae feed on various species of the family Compositae.

Nineteen specimens (11 ♂♂, 8 ♀♀) have been examined from nine localities in the following parishes: Catahoula, East Feliciana, Jackson, Lafayette (SLI), Orleans, St. Charles, St. Tammany, Washington and West Feliciana. Previously it had been recorded from Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863; Jung, 1939, 1950).

PRECIS EVARETE COENIA (HUBNER), the Buckeye.—This common butterfly of the southern states probably is familiar to everyone. In Louisiana it is very abundant throughout the spring, summer and autumn; earliest and latest dates are January 21, 1950 (1 ♂) and November 8, 1949 (1 ♂, 1 ♀). Of all that were collected in the state only a few were obtained while they were flying or feeding, for the insect seems to prefer to sit on hard, dry mud in full sunlight, slowly moving its wings. During a recent visit to Lacombe, La. the writer saw hundreds of buckeyes sitting on a large mound of dry, yellow clay.

Holland (1931) stated that the larvae in the later stages feed on plantains and Scudder (1889) reported them on *Gerardia purpurea* and on other species of the family Scrophulariaceae.

Forty-seven specimens (31 ♂♂, 16 ♀♀) have been examined from 31 localities in the following parishes: Allen, Claiborne, East Baton Rouge, Evangeline, Jefferson, Lafayette (SLI), Livingston, Natchitoches, Orleans, Ouachita, Rapides, St. Bernard, St. Charles, St. James, St. John the Baptist, St. Landry, St. Tammany, Tangipahoa, Union and Washington. Previously it had been recorded from Madison (Glick, 1939) and Orleans parishes (von Reizenstein, 1863; Jung, 1950).

LIMENITIS ARTHEMIS ASTYANAX (FABRICIUS), the Red-spotted Purple.—This butterfly is very fast in flight, and if disturbed will soar into the air. Most of the specimens were obtained in damp, swampy places where they often sit on soft mud, or upon the leaves of shrubs and small trees. The larvae feed on cherry, apple, hackberry, willow and related shrubs and trees (Holland, 1931).

The species flies throughout the summer and early fall; earliest and latest dates are May 31, 1949 (1 ♀) and October 15, 1949 (1 ♀).

Thirteen specimens (6 ♂♂, 7 ♀♀) have been examined from nine localities in the following parishes: Catahoula, Claiborne, East Feliciana, Livingston, Orleans, Tangipahoa, Terrebonne (LSM) and West Feliciana. Previously it had been recorded from St. Tammany parish by Jung (1950).

LIMENITIS ARCHIPPUS WATSONI (DOS PASSOS), the Viceroy.—This butterfly exhibits one of the best known examples of protective mimicry. It looks almost exactly like the monarch, *Danaus plexippus,* a species protected from insectivores by the unpleasant taste it possesses from feeding on milkweeds. An interesting fact concerning the viceroy is that throughout its range are found subspecies each of which mimics the prevalent danaid of the area (Chermock, 1947).

L. archippus ranges throughout North America into the Gulf States where the subspecies *floridensis,* in the east, and *watsoni,* in the west, occur. The latter was described by Dos Passos (1938) from specimens caught at Alexandria, La. In the state this subspecies is very common during the spring, summer and autumn months; earliest and latest dates are April 24, 1948 (1 ♂) and November 12, 1949 (1 ♀).

The flight, usually within five feet of the ground, is fast, but leisurely, and the butterfly is not too difficult to capture as it flies, or when it feeds on flowers. The larvae feed on various species of willows, although occasionally they feed on plum and cherry (Scudder, 1889).

Thirty-three specimens (24 ♂♂, 9 ♀♀), have been examined from 22 localities in the following parishes: Allen, Assumption, Claiborne, Evangeline, East Baton Rouge, Jefferson, Lafayette (SLI), Lafourche, Livingston, Orleans, Pointe Coupee, St. Bernard, St. Charles, St. Helena, St. James, St. Landry and Tangipahoa. Previously it had been recorded from Orleans (Jung, 1950), Rapides (Dos Passos, 1938) and Tensas parishes (Montgomery, 1932).

ANAEA ANDRIA (SCUDDER).—The Goatweed Butterfly is very common in Louisiana during the spring and early summer, but because of its rapid flight and protective coloration it is difficult to capture. Earliest and latest dates are February 2, 1929 (1 ♀) and October 20, 1939 (1 ♂). When resting this butterfly usually sits on the ground among dead leaves showing the under surfaces of the wings which blend well with the surroundings. Several individuals have been taken on the trunks of sycamore trees; others undoubtedly blended with the loose bark and were not seen. The caterpillars feed on the goatweed (*Croton capitatum*).

A. andria appears to be slightly more abundant in northern Louisiana. Most of the specimens were taken in the hardwood areas. Eighteen specimens (9 ♂♂, 9 ♀♀) were examined from 13 localities in the following parishes: Catahoula, Claiborne, Concordia, Evangeline (SLI), Lafayette (SLI), Morehouse, Orleans, Pointe Coupee, Winn and Union. Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932), Orleans (Jung, 1950) and Rapides parishes (Johnson and Comstock, 1941).

ASTEROCAMPA CLYTON CLYTON (BOISDUVAL AND LECONTE).—The Tawny Emperor is not very common in Louisiana. The writer has seen two females, and von Reizenstein (1863) and Jung (1950) reported it from New Orleans. The butterfly is very fast in flight and is difficult to catch. The larvae feed on leaves of the hackberry (*Celtis mississippiensis*).

The Louisiana records are: *Lafayette*: Lafayette, VII-20-41, 1 ♀ (SLI); *Ouachita*: Sterlington, VI-23-50, 1 ♀ (TU 2072).

ASTEROCAMPA CELTIS CELTIS (BOISDUVAL AND LECONTE).—In Louisiana the Hackberry Butterfly is very common during the hot summer months, but due to the difficulty of capturing it only a few have been taken. Earliest and latest dates are June 8, 1947 (1 ♂) and August 3, 1931 (1 ♂). The flight is exceptionally rapid, high around the tops of bushes and trees. The larval food is hackberry.

Twenty-one specimens (9 ♂♂, 12 ♀♀) have been examined from seven localities in the following parishes: Concordia, Lafayette (SLI), Ouachita, Richland, and Sabine. Previously it had been recorded from Orleans parish by von Reizenstein (1863) and Jung (1950).

ASTEROCAMPA CELTIS ALICIA (EDWARDS).—Apparently in Louisiana this subspecies of the hackberry butterfly is quite restricted in its range, whereas *A. celtis celtis* is the dominant subspecies throughout the state.

The writer saw many of these butterflies darting among the branches of hackberry trees along the Mississippi river batture near New Orleans. On that occasion two males were captured, but not without considerable effort. The three specimens examined were all taken in Orleans parish as follows: VII-10-32, 1 ♀ (TU P-982) and IX-1-48, 2 ♂♂ (TU 1258).

Family LIBYTHEIDAE

LIBYTHEANA BACHMANNII BACHMANNII (KIRTLAND), the Snout Butterfly.—This species is very abundant in Louisiana during the hot summer months, but appears to fly at least occasionally even during the winter as the writer has observed a few individuals in December and January. Other than these "off season" observations the earliest and latest dates are May 19, 1950 (1 ♂) and August 27, 1949 (1 ♂). They may be found in swarms along roadside pools of water and damp places on the ground. Williams (1937) described a southeasterly migration of these "snouts" in September, which extended over a front of 250 miles. He estimated that one and a quarter million butterflies passed every minute on the whole front. The larvae feed on hackberry trees.

Twenty-four specimens (17 ♂♂, 7 ♀♀) have been examined from 14 localities in the following parishes: Catahoula, Concordia, East Feliciana, Lafayette (SLI), Morehouse, Orleans, Sabine, St. Bernard, Vermilion (SLI), Washington and West Feliciana. Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932) and Orleans parishes (Jung, 1939, 1950).

Family RIODINIDAE

CALEPHELIS VIRGINIENIS (GUERIN), the Little Metal-mark.—The writer has captured a single male of this tiny butterfly from the Florida parish area, in the easternmost section of the state. Little is known of the immature stages of this species.

The lone record is: *St. Tammany*: St. Tammany, III-29-51, 1 ♂ (TU 2349). Previously it had been recorded from Opelousas in St. Landry parish by Holland (1931) under the synonym *C. louisiana.*

Family LYCAENIDAE

ATLIDES HALESUS HALESUS (CRAMER), the Great Purple Hair-streak.—The writer has not taken this beautiful insect, but Jung (1950) reported it from New Orleans. The one specimen examined was also collected in New Orleans, November 11, 1933, 1 ♂ (TU P-991).

STRYMON CECROPS (FABRICIUS).—The Cecrops Hair-streak is common in Louisiana during the spring and summer months, and is easily taken while it feeds on flowers. Earliest and latest dates are January 30, 1950 (1 ♂) and October 16, 1949 (1 ♂). A habit peculiar to the lycaenids consisting of "cleaning" or rubbing together the upper surfaces of the wings while at rest, is practiced strongly by this species.

Twelve specimens (10 ♂♂, 2 ♀♀) have been examined from twelve localities in the following parishes: Allen, East Feliciana, Franklin, Lafayette (SLI), Madison, Orleans, Ouachita, Pointe Coupee, Sabine, St. Tammany and Tangipahoa. Previously it had been recorded from Caddo (Field, 1941) and Madison parishes (Montgomery, 1932).

STRYMON MELINUS MELINUS (HUBNER), the Common Hair-streak.—This species is very common in Louisiana. The butterfly is very

swift in flight but is taken easily while feeding on wild flowers. It flies throughout the spring, summer and early fall; earliest and latest dates are March 10, 1943 (1 ♂) and October 14, 1949 (1 ♀). Howard (1895) described the damage to bean plants caused by the larvae.

Twenty-three specimens (15 ♂♂, 8 ♀♀) have been examined from 16 localities in the following parishes: Catahoula, Evangeline, Jefferson, Lafayette (SLI), Lincoln, Livingston, Natchitoches, Orleans, St. Bernard, St. Tammany, Tangipahoa and Washington. Previously it had been recorded from Cameron (Hine, 1906) and Orleans parishes (Jung, 1950).

STRYMON ONTARIO AUTOLYCUS (EDWARDS).—The Northern Hairstreak has been taken only once in Louisiana. Klots (1951) stated that it is not common, but may be caught easily while it feeds. The larva feeds on oak.

S. ontario autolycus has not been recorded from Louisiana previously. The Louisiana record is: *Orleans:* New Orleans, V-5-51, 1 ♀ (TU 3010).

STRYMON LIPAROPS LIPAROPS (BOISDUVAL AND LECONTE), the Striped Hair-streak.—Scudder (1889) stated that this butterfly is usually localized near thickets and swamps. The only specimen from Louisiana was taken in a dense upland hardwood forest with a very thick undergrowth of vines.

S. liparops liparops has not been recorded from Louisiana previously. The lone record is: *LaSalle*: Summerville, VI-12-50, (TU 2049).

INCISALIA IRUS (GODART), the Hoary Elfin.—This species is included on the basis of Skinner's report (1907), of it from the state, although the record is rather dubious. Holland (1931) stated that the species is always rather rare, but has a wide east-west distribution in the latitude of New England. This means that Skinner either published an exceptional range extension, or that he was confused with other nearly related species; most likely his specimen was *I. henrici,* with which *irus* has often been confused.

FENISECA TARQUINIUS TARQUINIUS (FABRICIUS), the Harvester.—The writer has taken only one specimen of this species, a female which was captured in a dense hardwood forest on the banks of the Ouachita river in northeastern Louisiana. The butterfly was flying about four feet from the ground in a very nervous manner and was taken with difficulty. The larvae of this butterfly are of some economic importance because they feed on woolly aphids, particularly those of the alder and beech.

The single record is: *Richland*: 7 miles north of Girard, VI-27-50, 1 ♀ (TU 2084). Previously the species was recorded from Caddo (Scudder, 1889), Orleans (von Reizenstein, 1863) and Webster parishes (Johnson, 1886).

HEMIARGUS ISOLUS (REAKIRT), Reakirt's Blue.—Klots (1951)

gives the range as "Mexico, north to Nebraska, almost entirely west of the Mississippi river." The few specimens collected in Louisiana certainly appear to be at the eastern edge of the species' range, and may be considered an extension as far as the southern portion of the range is concerned.

H. isolus has not been recorded from Louisiana previously. The records are: *Concordia*: 13 miles northwest of Ferriday, VI-16-50, 1 ♂ (TU 2056); *Morehouse*: 12 miles east of Mer Rouge, VI-19-50, 3 ♂♂, 1 ♀ (TU 2063).

EVERES COMYNTAS COMYNTAS (GODART).—The Eastern Tailed-blue is very abundant in Louisiana during the spring and summer months; earliest and latest dates are January 2, 1950 (1 ♀) and October 14, 1949 (1 ♂). The writer has seen most specimens along the edges of forests in partly shaded areas and on the ground around moist places. Their quick flight and small size make them hard to catch.

Sixty-five specimens (38 ♂♂, 27 ♀♀) have been examined from 25 localities in the following parishes: Catahoula, Evangeline, East Feliciana, Lafayette (SLI), LaSalle, Lincoln, Madison, Morehouse, Natchitoches, Ouachita, Richland, Sabine, St. Charles, St. Tammany, Union, Washington and West Carroll. Previously it had been recorded from Madison parish by Montgomery (1932).

CELASTRINA ARGIOLUS PSEUDARGIOLUS (BOISDUVAL AND LECONTE).—The Spring Azure apparently is rare in Louisiana. The few specimens collected were taken in the longleaf pine flats of the Florida parishes. Scudder (1889) stated that the range does not touch the Gulf of Mexico; hence this species may not be found in the coastal parishes.

C. argiolus pseudargiolus has not been recorded from Louisiana previously. The two records are *East Feliciana*: Felixville, VI-8-50, 3 ♂♂ (TU 2037); *Washington*: Angie, VI-4-50, 1 ♂ (TU 2032).

Family PAPILIONIDAE

PAPILIO POLYXENES ASTERIAS (STOLL).—The Common American Swallowtail apparently is not confined to any particular part of Louisiana. It is rather abundant throughout the spring and summer; earliest and latest dates are January 1, 1950 (1 ♂) and September 7, 1926 (1 ♀). It is a frequent visitor to flowers; specimens have been taken on roses, clover and numerous umbelliferous plants. It has some economic importance as the caterpillars may feed on celery, dill, parsnip, carrots, caraway and parsley.

Twenty-three specimens (14 ♂♂, 9 ♀♀) have been examined from ten localities in the following parishes: Claiborne, Franklin, Jefferson, Lafayette (SLI), Orleans, Richland, St. Charles, Tensas, Vermilion (SLI) and Washington. Previously it had been recorded from Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863; Jung, 1939, 1950.

PAPILIO CRESPHONTES CRESPHONTES (CRAMER).—The Giant Swallowtail, one of largest of the North American butterflies, is of eco-

nomic importance to fruit growers for the caterpillar, the "Orange-puppy," feeds on citrus trees. In Louisiana it is more abundant in the southernmost areas. Rothschild and Jordan (1906) record the species from "Louisiana."

Saverner (1908) reported badly damaged *P. cresphontes* and *P. troilus* migrating southward along with monarchs during August; this may have been the situation of two *cresphontes* captured in north Louisiana during August which were accompanying a southerly migration of monarchs. In Louisiana the species flies from spring to early fall; earliest and latest dates are March 2, 1949 (1 ♂, 1 ♀) and November 13, 1911 (1 ♀).

Twenty-six specimens, (13 ♂♂, 13 ♀♀) have been examined from eleven localities in the following parishes: Claiborne, Jefferson, Lafayette (SLI), Livingston, Orleans, Plaquemines, St. Tammany, Terrebonne (LSM) and Vermilion (SLI). Previously it had been recorded from Cameron (Hine, 1906) Orleans (von Reizenstein, 1863; Jung, 1939, 1950) Plaquemines (Jung, 1950), St. Bernard (Jung, 1950) and Terrebonne parishes (Comstock, 1882).

PAPILIO GLAUCUS GLAUCUS (LINNÉ).—The Tiger Swallowtail displays strong sexual dimorphism. In the southern part of its range some of the females are dark brown rather than black and yellow. According to Klots (1951) this melanism occurs in about 50 percent of the females, but he states that the brown form is less common or nonexistent in the extreme south. All of the females that the writer has seen from Louisiana show this dark brown coloration. Some of the males are larger and tend to show the darker yellow color of *P. glaucus australis,* although none of the specimens appear clearly to be that subspecies.

The species is a strong flier and is difficult to catch in flight; however, the writer found them easy to collect while they were feeding on the thistle (*Cirsium horridulum*). Riley and Howard (1895) reported the caterpillars feeding on the leaves of camphor trees in Louisiana.

The species has been collected in all months of the year except January and December; earliest and latest dates for adults are February 18, 1950 (2 ♂♂) and November 16, 1939 (1 ♀).

Twenty-three specimens (17 ♂♂, 6 ♀♀) have been examined from twelve localities in the following parishes: Assumption, Bossier, Claiborne, Lafayette (SLI), Madison, Morehouse, Natchitoches, Orleans, Sabine, St. Charles, St. Tammany and Washington. Previously it had been recorded from Jefferson (Jung, 1950), Morehouse (Riley and Howard, 1895), Orleans (von Reizenstein, 1863) and St. Tammany parishes (Jung, 1950).

PAPILIO TROILUS TROILUS (LINNÉ).—The Spicebush Swallowtail is the most common member of its genus in Louisiana. It flies from early spring to late summer; earliest and latest dates are February 23, 1949 (3 ♂♂) and September 16, 1945 (1 ♂). The larvae and adults feed on spicebush, sassafras and other Lauraceae.

Saverner (1908) stated that *P. troilus* was seen migrating southward with the monarch (*Danaus plexippus*) in August, but no evidence of migrations of this swallowtail have been noted as yet in Louisiana.

Forty-one specimens (27 ♂♂, 14 ♀♀) have been examined from eleven localities in the following parishes: Caddo, DeSoto, Jackson, Jefferson, Lafayette (SLI), LaSalle, Orleans, Ouachita, Sabine, St. Tammany and Union. Previously it had been recorded only from Orleans parish by von Reizenstein (1863) and Jung (1939, 1950).

PAPILIO TROILUS ILIONEUS J. E. SMITH.—While many of the spicebush swallowtails from Louisiana are more typical of the subspecies *troilus,* three specimens possess very definite characteristics of subspecies *ilioneus.* However, the majority collected have characteristics common to either or both of the subspecies, due to the clinal nature of the species.

P. troilus ilioneus has not been recorded from Louisiana previously. The records are: *Orleans:* New Orleans, III-4-49, 2 ♀♀ (TU 1110); *Ouachita:* Sterlington, VI-23-50, 1 ♂ (TU 2072).

PAPILIO PALAMEDES PALAMEDES (DRURY).—The Palamedes Swallowtail is a rather rare insect in Louisiana, records of this species being confined to the coastal parishes. As this butterfly is a strong flier and difficult to capture, adults are more readily obtained by rearing them from the larval stage. The few specimens collected were taken in the months of April, June, July, August and October; earliest and latest dates are April 1, 1918 and October 13, 1934.

Nine specimens (5 ♂♂, 4 ♀♀) were examined from three localities in the following parishes: Lafayette (SLI), Orleans and Terrebonne (LSM). Previously it had been recorded from Orleans parish by von Reizenstein (1863), Rothschild and Jordan (1906) and Jung (1950).

GRAPHIUM MARCELLUS MARCELLUS (CRAMER), the Pawpaw Butterfly.—Although this species is fairly common in Louisiana during the early summer months it is exceedingly difficult to take with a net. A few specimens were obtained, however, after many others had eluded capture. Earliest and latest dates were April 1, 1950 (1 ♂) and September 10, 1947 (1 ♀). Late in the survey it was learned that this butterfly usually picks an orbit to follow in its flight, and if the collector misses it on the first try he has only to wait a few minutes for the same individual to return, flying almost exactly the same course.

Within Louisiana *marcellus* apparently is rare in the coastal and Florida parish areas, and all of the specimens were obtained from the vicinity of the Mississippi river westward and northward. It is more abundant in the upland areas of the state. Its scarcity in southern Louisiana may be due to the lack of its food plant, the pawpaw (*Asimine triloba* and *A. parviflora*), in the coastal region.

Eleven specimens (6 ♂♂, 5 ♀♀) were examined from five local-

ities in the following parishes: Catahoula, Lafayette (SLI), Sabine, Union and West Feliciana. Previously it had been recorded from Orleans parish by Kopman (1903) under the name *Papilio ajax.*

BATTUS PHILENOR PHILENOR (LINNÉ).—The Pipe-vine Swallowtail is most common during the summer months in Louisiana, but it has a long flying season; earliest and latest dates are February 1, 1949 (1 ♂) and October 16, 1940 (1 ♀). Holland (1931) states that *philenor* has been observed ovipositing as late as October. The species is exceptionally fast in flight, perhaps accounting for the scarcity of records. The larvae generally feed on Dutchman's pipe or pipe-vine (*Aristolochia serpentaria* and *A. durior*).

Seventeen specimens (13 ♂♂, 4 ♀♀) have been examined from eleven localities in the following parishes: Bossier, Lafayette (SLI), Morehouse, Ouachita, Rapides, Sabine, St. Tammany, Union and Washington. Previously it had been recorded from Cameron (Hine, 1906), Orleans (von Reizenstein, 1863), St. John the Baptist (Jung, 1950), St. Mary (Kopman, 1903), and St. Tammany parishes (Jung, 1950).

BATTUS POLYDAMUS LUCAYUS (LINNÉ), the Polydamus Butterfly.—The writer has not seen this butterfly in Louisiana, but von Reizenstein (1863) reported it from New Orleans. According to his observations it was very rare, usually found feeding on Virginia snake root and Dutchman's pipe. McDunnough (1938) doubted its occurrence in North America, but Klots (1951) stated that it occurs in the Gulf states from Florida to Texas.

Family PIERIDAE

ANTHOCHARIS GENUTIA GENUTIA (FABRICIUS), the Falcate Orangetip.—In Louisiana this species apparently is confined to the upland regions of the northern part of the State. Scudder (1889) stated that the butterfly has never been very abundant. From the writer's experience it seems that this species is a very weak flier, and is easy to collect, although Scudder (1889) reported otherwise.

A. genutia has not been recorded from Louisiana previously. The three records are: *Jackson:* Kelleys, IV-1-50, 1 ♂ (TU 1846); Chatham, IV-1-50, 2 ♂♂ (TU 1849); *Lincoln:* Downsville, IV-1-50, 1 ♂, 1 ♀ (TU 1859).

COLIAS EURYTHEME EURYTHEME BOISDUVAL.—The Eurytheme Sulphur can be found in all parts of Louisiana, but it is not as abundant in the coastal area as it is in the pinelands and uplands, especially in open grass or clover-covered fields. This species flies throughout most of the year; earliest and latest dates are January 21, 1950 (2 ♂♂) and November 8, 1939 (1 ♀). The larvae feed occasionally on *Trifolium repens* and other related species of this genus, but Scudder (1889) reported that the caterpillars would not eat red clover. The favorite food, however, is the introduced alfalfa (*Medicago sp.*), on which it is a serious pest.

With the exception of *C. a. pseudargiolus,* a lycaenid, *C. eurytheme*

is probably the most variable species in our butterfly fauna. The literature is filled with descriptions of the many sexual and seasonal forms. These have been considered at times to be distinct species, and as such have presented a very puzzling problem. However, in recent years much has been done by Hovanitz (1943, 1944) to study the *Colias* complex; hybridization and female albinism have been studied also by Gerould (1946).

Sixty specimens (26 ♂♂, 34 ♀♀) have been examined from 22 localities in the following parishes: Assumption, Claiborne, Concordia, East Baton Rouge, Evangeline, Lafayette (SLI), Morehouse, Natchitoches, Orleans, Ouachita, Rapides, Richland, and St. Charles. Previously it had been recorded from East Baton Rouge (Floyd, 1941), Madison (Montgomery, 1932; Glick, 1939) and Orleans parishes (Scudder, 1889; Jung, 1939, 1950).

COLIAS PHILODICE PHILODICE (LATREILLE), the Common Sulphur.—The common name of this butterfly implies abundance, but it is rather rare in Louisiana, and although it has a wide range throughout North America one specimen has thus far been taken in the state. From what can be discerned from Scudder (1889) it is not numerous at the southern extremities of its range.

C. philodice philodice has not been recorded from Louisiana previously. The lone record is: *Lafayette:* Lafayette, XI-30-36, 1 ♂ (SLI).

ZERENE CESONIA (STOLL), the Southern Dog-face.—The writer has examined only one specimen from Louisiana, and it has been recorded by von Reizenstein (1863) from New Orleans. The fact that this butterfly flies very fast and often high off the ground may account for the scarcity of records. The species frequents pinelands, and has been seen by the writer in the pine flats of the Florida parishes in August, but on that occasion the individuals were flying fast and high above the ground, and none were caught.

The single record is: *Lafayette:* Lafayette, XI-12-28, 1 ♂ (SLI).

PHOEBIS SENNAE EUBULE (LINNÉ).—The Cloudless Sulphur is very abundant during most of the year throughout Louisiana. Earliest and latest dates are March 4, 1934 (1 ♀) and November 1, 1949 (1 ♂). It is an exceptionally strong flier, and is migratory. Great swarms of them have been observed far out at sea, flying just above the waves (Williams, 1937). During courtship when the male and female "pinwheel" high above the ground they are especially hard to capture, yet when feeding they are so occupied that the writer has taken many by hand. The larvae feed on *Cassia* spp.

Forty-six specimens (25 ♂♂, 21 ♀♀) have been examined from 32 localities in the following parishes: Allen, Assumption, Bossier, Claiborne, Concordia, East Baton Rouge, Evangeline, Franklin, Jefferson, Lafayette (SLI), Orleans, Ouachita, Pointe Coupee, Rapides, Red River, Richland, Sabine, St. Bernard, St. Helena, St. Tammany, Tangipahoa (SLI, TU) and Washington. Previously it had been recorded from Madison (Montgomery, 1932) and Orleans parishes

(von Reizenstein, 1863; Jung, 1939, 1950).

PHOEBIS SENNAE SENNAE (LINNÉ).—This subspecies is included on the basis of Klots' (1951) mention that "in southern Florida and Louisiana many very *sennae*-like specimens occur." He describes the color as being a warmer yellow than that of *eubule.* Indeed, in the Tulane and Southwestern Louisiana Institute collections there are specimens of *P. sennae* that fit this description, particularly those from the Lafayette area. Since the subspecific classification is very complex and for the most part a matter of statistics the writer has chosen to include the "*sennae*-like" specimens in the records for *eubule.* One female taken at Lafayette on November 2, 1950 comes closest to fitting the description of warm yellow.

PHOEBIS PHILEA (LINNÉ), the Red-barred Sulphur.—The writer has never collected *P. philea* although several specimens from Louisiana have been available for examination. In addition to these the writer has information from Dr. Wm. T. M. Forbes (in personal communication) that he had taken this species in New Orleans on January 1, 1933. The species is known to be migratory.

P. philea has not been recorded from Louisiana previously. The few records are: *Allen:* Kinder, VI-12-41, (SLI); *Orleans:* New Orleans, X-11-32, 1 ♂ (TU P-978), and VII-15-32, 1 ♀ (TU P-982).

PHOEBIS AGARITHE MAXIMA (NEUMOEGEN), the Large Orange Sulphur.—As this butterfly is mainly tropical, only three specimens have been caught in Louisiana, and these are from the southern parishes. The species is migratory according to Williams (1937).

It has not been recorded from the state previously. The few records are: *Lafayette:* Lafayette, 1 ♀ (SLI); *Orleans:* New Orleans, VIII-24-26, 1 ♀ (TU P-965), IX-19-31, 1 ♀ (TU P-977), and X-2-31, 1 ♀ (TU P-978).

EUREMA DAIRA DAIRA (LATREILLE), the Fairy Yellow.—This is a very variable species; some have all, others only one-half the border of the hind wings black, and individuals of the latter type often have the undersides of the hind wings white. These two forms for a long time were held as two species, but Dr. R. L. Chermock (personal correspondence) considers them to be variations of one species.

In Louisiana the species apparently is not widespread, nor does it fly during as great a part of the year as does *E. lisa.* With the exception of one male from the southwest, all specimens were taken during the summer in the Florida parishes. Though the species apparently is not evenly distributed, the writer found a dense population of what appeared to be a southwesterly migration September 6-8, 1950, near Covington, La. All the butterflies were flying in one direction a few feet from the ground stopping only occasionally to feed at conspicuous flowers.

E. daira daira has not been recorded previously from Louisiana.

The records are: *Lafayette:* Lafayette, IX-25-36, 1 ♂ (SLI); *Livingston:* Springfield, IX-6-50, 2 ♂♂, 1 ♀ (TU 2183, 2184); *St.*

Helena: Liverpool, IX-7-50, 3 ♂♂, 1 ♀ (TU 2193); Greensburg, IX-7-50, 2 ♂♂ (TU 2194); *St. Tammany:* Folsom, IX-7-50, 1 ♂, 2 ♀♀ (TU 2187); Covington, IX-8-50, 2 ♂♂ (TU 2196); *Tangipahoa:* Lee Landing, IX-6-50, 1 ♂ (TU 2181); Robert, IX-6-50, 1 ♂, 1 ♀ (TU 2185); Tangipahoa, IX-7-50, 1 ♀ (TU 2191); Amite, IX-7-50, 2 ♀♀ (TU 2195); *Washington:* Angie, VI-5-50, 1 ♂, 1 ♀ (TU 2034); Richardson, IX-7-50, 1 ♂, 2 ♀♀ (TU 2188).

EUREMA NICIPPE NICIPPE (CRAMER).—The Nicippe Sulphur is common throughout Louisiana during most of the summer months. However, it has a relatively long flying season; earliest and latest dates are April 8, 1950 (1 ♀) and December 8, 1949 (1 ♀).

This butterfly is not usually common everywhere throughout the summer, but occurs in small swarms in sunny places in the pinelands. When it is flying it is rare to see only one at a time, as usually several are in flight short distances from each other.

Forty-eight specimens (30 ♂♂, 18 ♀♀) have been examined from 26 localities in the following parishes: Avoyelles (SLI), Catahoula, Claiborne, Concordia, Evangeline, Lafayette (SLI), Livingston, Morehouse, Ouachita, Plaquemines, Pointe Coupee, Rapides, Richland, Sabine, St. Helena, St. Landry (SLI), St. Tammany, Tangipahoa, Vermilion (SLI) and Washington. Previously it had been recorded from Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863).

EUREMA LISA (BOISDUVAL AND LECONTE).—The Little Sulphur is the most abundant pierid in the state. In Louisiana it is most abundant in mid-summer, although it flies from early spring well into the autumn. Earliest and latest dates are January 2, 1950 (2 ♀♀) and October 16, 1949 (4 ♂♂, 4 ♀♀). Scudder (1889) stated that the butterfly will fly in heavily clouded weather, but the writer believes this to be unlikely as it has always been observed to take cover when clouds hide the sunlight.

E. lisa is not a strong flier and is easy to capture. Usually they fly close to the ground in open places, and congregations of them are often seen sucking water from moist ground. However, in spite of its frailness and weak flight, it has been known to migrate in great clouds for remarkable distances (Scudder, 1889). The larvae feed on *Cassia* spp.

One hundred and eleven specimens (73 ♂♂, 38 ♀♀) have been examined from 56 localities in the following parishes: Allen, Assumption, Bienville, Catahoula, Claiborne, Concordia, DeSoto, Evangeline, Franklin, Lafayette (SLI), Lafourche, Livingston, Morehouse, Natchitoches, Orleans, Pointe Coupee, Rapides, Richland, Sabine, St. Bernard, St. Charles, St. Helena, St. Landry, St. Tammany, Tangipahoa, Washington, Webster and West Feliciana. Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932) and Orleans parishes (Jung, 1950).

NATHALIS IOLE (BOISDUVAL), the Dwarf Yellow.—Jung (1950) reported this species as very common about fields in New Orleans,

but I have not found it in great numbers at any one time as it is very local and easily overlooked. It flies in sunny, grassy places along the sides of roads, and in open fields. It is most abundant in the warmer months, but stragglers have been taken as late as October in Louisiana.

The few records are: *Claiborne:* 8 miles east of Lisbon, VIII-6-49, 1 ♂, 1 ♀ (TU 1457); *Lafayette:* Lafayette, X-2-36, 1 ♀ (SLI); *Pointe Coupee:* McCrea, X-14-49, 1 ♂ (TU 1568); *Sabine:* Negreet, VII-7-50, 1 ♀ (TU 2101); 10 miles west of Negreet, VII-8-50, 1 ♀ (TU 2106).

PIERIS RAPAE (LINNÉ).—The Cabbage Butterfly was not originally a member of the North American fauna, but was introduced on this continent at Quebec in 1860 from Europe. From there the species has spread throughout the continent inflicting damage to crops totalling hundreds of thousands of dollars annually. Scudder (1889) gave an excellent account of its spread, but gave no definite date for its introduction into Louisiana. However, it had reached Bastrop, Texas by 1881.

In Louisiana the species is abundant during the spring and early summer months, but may be seen flying during late fall and winter. Earliest and latest dates are January 2, 1950 (5 ♂♂, 1 ♀) and November 30, 1950 (1 ♂). The writer has seen many adults feeding on the blossoms of clover (*Trifolium repens*).

Twenty-one specimens (13 ♂♂, 8 ♀♀) have been examined from nine localities in the following parishes: Catahoula, Lafayette (SLI), Ouachita, St. Charles, Washington and West Feliciana. Previously it had been recorded from Orleans and St. Bernard parishes by Jung (1939, 1950).

PIERIS PROTODICE PROTODICE (BOISDUVAL AND LECONTE).—The Common White has a wide range over the continent and it is not scarce in Louisiana where it flies during the hot summer months. Earliest and latest dates are June 16, 1950 (5 ♂♂, 1 ♀) and September 5, 1938 (1 ♀). The flight is easy and rather methodical, and adults are easily collected.

Twelve specimens (8 ♂♂, 4 ♀♀) have been examined from seven localities in the following parishes: Catahoula, Concordia, Lafayette (SLI), Morehouse, Orleans and Ouachita. Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863; Jung, 1939, 1950).

ASCIA MONUSTE PHILETA (FABRICIUS), the Great Southern White.—Much has been written concerning the migration and immature stages of this butterfly by Nielsen and Nielsen (1950) who found eggs deposited on saltwort (*Batis maritima*), nasturtium (*Tropaeolum majus*), spider-wisp (*Cleome* spp.) and other plants. In spite of its wide range and abundance in the Gulf states only two males and one female have been caught in the state. However, the writer saw many of them flying along the shore and over the water of Lake Pontchartrain at New Orleans (May 10, 1950), but speci-

mens were not obtained.

The few records are: *Lafayette:* Lafayette, VI-25-28, 1 ♀ (SLI) and VII-8-50, 1 ♂ (SLI); *Orleans:* New Orleans, VI-30-31, 1 ♂ (TU P-974). Previously it had been recorded from Orleans parish by von Reizenstein (1863) and Jung (1939, 1950).

Superfamily HESPEROIDEA, the Skippers
Family HESPERIIDAE

EPARGYREUS CLARUS (CRAMER), the Silverspotted Skipper.—The flight of this species is very fast, and although it is common it is not easily caught. All specimens were captured while they fed on flowers, particularly blossoms of the buttonball bush (*Cephalanthus occidentalis*). Caterpillars feed on *Robina, Wisteria, Pueraria* and other leguminous plants.

Jung (1950) reported it common within residential New Orleans, but the writer has taken specimens only in sunny fields and bordering areas of woods.

The few Louisiana records are: *Caldwell:* Columbia, VIII-3-48, 1 ♂ (TU 429); *Sabine:* Negreet, VII-7-50, 1 ♂ (TU 2101); *St. Tammany:* Folsom, IX-7-50, 1 ♂ (TU 2187); Covington, IX-8-50, 1 ♂, 1 ♀ (TU 2196). Previously it had been recorded from Madison (Glick, 1939) and Orleans parishes (von Reizenstein, 1863; Jung, 1950).

URBANUS PROTEUS (LINNÉ), the Longtailed Skipper.—In Louisiana this species is seen almost throughout the year flying from flower to flower in open sunny places. Earliest and latest dates are February 23, 1949 (1 ♂) and November 6, 1949 (1 ♂). This skipper often picks a resting place and returns to the same spot time and time again after being disturbed. One such individual, whose tails were broken in such a way as to make it easily recognizable, favored a lead pipe in the writer's garden. Day after day for almost a month the same skipper headquartered around the pipe, occasionally flying a few feet away to feed on lantana flowers. The larvae feed on certain species of the Leguminosae, particularly *Wisteria* and *Clitoria.*

Twelve specimens (10 ♂♂, 2 ♀♀) have been examined from eight localities in the following parishes: Allen, Assumption, Orleans, Pointe Coupee, St. Bernard, St. Charles, St. Tammany and Tangipahoa. Previously it had been recorded from Orleans parish by Shufeldt (1884) and Jung (1950).

ACHALARUS LYCIADES (GEYER), the Hoary-edge.—Only three individuals have been taken in Louisiana, and these during the summer. One was captured while it was feeding on flowers of the buttonball bush (*Cephalanthus occidentalis*). The larvae feed on various leguminous plants.

The species has not been recorded from Louisiana previously. The few records are: *Sabine:* Negreet, VII-7-50, 1 ♂ (TU 2102); 10 miles west of Negreet, VII-8-50, 1 ♂ (TU 2106); *Union:* Marion, VI-24-50, 1 ♂ (TU 2075).

THORYBES BATHYLLUS (J. E. SMITH).—The Southern Dusky-wing is more abundant in Louisiana that its ally, *T. confusis,* and flies from early spring throughout the summer. Earliest and latest dates are February 24, 1950 (1 ♂) and September 8, 1950 (2 ♂♂, 1 ♀). The larvae feed on various species of the family Fabaceae.

T. bathyllus has not been recorded from Louisiana previously. The ten specimens examined (6 ♂♂, 4 ♀♀) are from the following localities: *Bienville:* Bienville (TU 1459); *Sabine:* Negreet (TU 2101); *St. Tammany:* Hickory (TU 1800); Covington (TU 2196); *Tangipahoa:* Ponchatoula (TU 2182); Robert (TU 2185); *Union:* 7 miles east of Farmerville (TU 1863); *Washington:* Richardson (TU 2188).

THORYBES CONFUSIS BELL.—The Northern Dusky-wing is found occasionally in Louisiana during the summer months but records of it are not numerous. According to Scudder (1889) it frequents open fields and sunny places visiting flowers, often clovers. Little is known of the immature stages.

T. confusis has not been recorded from Louisiana previously. The few records are: *Catahoula:* 5 miles southwest of Lee Bayou, VI-11-50, 1 ♀, (TU 2044); *Claiborne:* Scottsville, VI-29-50, 1 ♂ (TU 2086); *Sabine:* Belmont, VIII-2-49, 1 ♂ (TU 1379); Negreet, VII-10-50, 1 ♂ (TU 2103).

PYRGUS COMMUNIS COMMUNIS (GROTE).—The Common Checker-spot Skipper is one of the commonest skippers of Louisiana, often seen flying a few inches from the ground on hot, dusty roads. Earliest and latest dates are January 24, 1950 (1 ♂) and October 16, 1949 (3 ♂♂). Most specimens have been taken during flight, which is very rapid and elusive. The collector must not lose sight of the insect for a second if he wishes to catch it, for its checkerboard pattern blends very well with the background.

There is no apparent localization in the state, the species having been collected in all the major areas. The larvae feed on various species of the family Malvaceae.

Twenty-one specimens (18 ♂♂, 3 ♀♀) have been examined from 18 localities in the following parishes: Catahoula, East Feliciana, Evangeline, Jefferson, Lafayette (SLI), Natchitoches, Orleans, Ouachita, Pointe Coupee, Rapides, Sabine, St. Bernard, St. Charles, St. Landry, St. Tammany, Washington and West Feliciana. Previously it had been recorded from Orleans parish by Jung (1950).

CELOTES NESSUS (EDWARDS), the Streaky Skipper.—The writer has not seen this species in Louisiana but it was reported from Madison parish by Glick (1939) who did extensive work with traps carried by airplanes. A single specimen was taken during the day at an altitude of twenty feet.

PHOLISORA HAYHURSTII (EDWARDS), Hayhurst's Skipper.—A single specimen of this species has been taken in Louisiana, flying near the ground in a dense oak-hardwood stand on the front lands of the

Mississippi river. Little is known concerning the immature stages.

The species has not been recorded from Louisiana previously. The single record is: *Jefferson:* Kenner, III-9-51, 1 ♂ (TU 2298).

ERYNNIS HORATIUS (SCUDDER AND BURGESS), Horace's Dusky-wing.—Most of the individuals were captured in hot, sunny spots in and along dense forests, but none were seen feeding. The flight is rapid and fleeting, the insect staying about ten feet away from the collector, alighting on the ground, and darting to a new resting place if disturbed. Three males collected on June 4th, and 5th were sitting on the hot, dry surface of a sand bar along the Pearl river. Earliest and latest dates are June 1, 1950 (1 ♂) and September 7, 1950 (1 ♂). Little is known about the immature stages.

Eleven specimens (9 ♂♂, 2 ♀♀) were examined from nine localities in the following parishes: Assumption, DeSoto, East Feliciana, LaSalle, St. Tammany, Union and Washington. Previously it had been recorded from Orleans parish by Jung (1950).

ERYNNIS JUVENALIS (FABRICIUS).—Only three specimens of this skipper have been taken in Louisiana. The larvae feed on oaks and various legumes according to Scudder (1889).

This species has not been recorded from Louisiana previously. The records are: *Orleans:* New Orleans, II-4-50, 1 ♀ (TU 1782); *St. Tammany:* Covington, IX-8-50, 2 ♀♀ (TU 2196).

ANCYLOXYPHA NUMITOR (FABRICIUS).—The Numitor Skipperling apparently is never abundant in Louisiana. According to Scudder (1889) the flight is slow and feeble and it is one of the easiest skippers to capture in flight. The larvae feed on grasses (Klots, 1951). Earliest and latest dates are February 18, 1950 (1 ♂) and October 19, 1949 (1 ♀).

Eight specimens (3 ♂♂, 5 ♀♀) have been examined from seven localities in the following parishes: Allen, Evangeline, Jefferson, St. Bernard, St. Charles, St. Tammany and Washington. Previously it had been recorded from Jefferson parish by Jung (1950).

COPAEODES MINIMA (EDWARDS), the Tiny Skipperling.—This is probably the smallest skipper in North America. It is very common but its size and ability to blend into its surroundings make it difficult to see. The majority were taken while feeding on daisies in open, sunny fields throughout the state. Earliest and latest dates are March 2, 1949 and October 18, 1949. Nothing is known of the early stages.

C. minima has not been recorded from Louisiana previously. Twenty-four specimens (13 ♂♂, 11 ♀♀) have been examined from 14 localities in the following parishes: Claiborne, Evangeline, Jefferson, Livingston, Morehouse, Orleans, Ouachita, Pointe Coupee, Rapides, Richland, St. Bernard and Tangipahoa.

HESPERIA LEONARDUS STALLINGSI H. A. FREEMAN.—A single specimen of the Leonardus Skipper was taken in Madison parish by Glick (1939) in an airplane trap at an altitude of twenty feet. The

writer has no other information concerning the occurrence of this species in Louisiana.

HYLEPHILA PHYLEUS (DRURY).—The Fiery Skipper is often taken while it frequents flowers along the borders of woods, and in open places in dense forests. The flight is not rapid, hence the species is easily captured. Earliest and latest dates are March 2, 1949 (1 ♀) and October 16, 1949 (1 ♂, 1 ♀). The larvae supposedly feed on crab grass (Scudder, 1889).

Twenty-one specimens (13 ♂♂, 8 ♀♀) have been examined from 15 localities in the following parishes: Catahoula, East Feliciana, Evangeline, Jefferson, Morehouse, Orleans, Richland, Sabine, St. Landry, Tangipahoa, Union and Washington. Previously it had been recorded from Cameron parish by Hine (1904).

ATALOPEDES CAMPESTRIS (BOISDUVAL), the Sachem.—The few Louisiana specimens are all from the eastern parishes near the Mississippi river. From what the writer has observed the flight is rather rapid and jerky, the skipper flitting from flower to flower; however, when it is feeding it may be caught easily. The larvae feed on Bermuda grass.

The species has not been recorded from Louisiana previously. The records are: *East Feliciana:* Felixville, VI-8-50, 2 ♀♀ (TU 2039); *LaSalle:* Summerville, VI-12-50, 1 ♂ (TU 2048); *Morehouse:* 10 miles west of Twin Oaks, VI-26-50, 1 ♂, 1 ♀ (TU 2079); *Ouachita:* Perryville, VI-23-50, 1 ♂ (TU 2071); Sterlington, VI-18-50, 1 ♂ (TU 2060) and VI-23-50, 1 ♀ (TU 2072); *Union:* Marion, VI-24-50, 1 ♂, 1 ♀ (TU 2075).

POLITES MANATAAQUA MANATAAQUA (SCUDDER), the Manataaqua Skipper.—Lindsey, Bell and Williams (1931) stated that this subspecies occurs from the northeastern United States to Alabama, and westward to South Dakota and Nebraska. Klots (1951) described its range as above, but included Arkansas and Georgia. The species is rare in Louisiana, but nevertheless the six specimens taken constitute what appears to be a southern range extension. All were captured in moist, grassy openings in the pine flats of the Florida parishes north of Lake Pontchartrain. The larvae feed on common grasses.

The subspecies has not been recorded from Louisiana previously. The records are: *St. Tammany:* Hickory, IX-13-50, 1 ♂ (TU 2198); *Tangipahoa:* Ponchatoula, IX-6-50, 4 ♂♂, 1 ♀ (TU 2182).

POLITES THEMISTOCLES (LATREILLE).—The Tawny-edged Skipper is well distributed throughout Louisiana. All specimens thus far have been collected during the summer months in open sunny spots in fields and woods, especially where there are flowers in bloom. The caterpillars feed on grass.

The species has not been recorded from Louisiana previously. The records are: *East Feliciana:* Felixville, VI-8-50, 1 ♂ (TU 2039); *Sabine:* Negreet, VII-7-50, 1 ♀ (TU 2101); *St. Tammany:* Hickory,

VII-15-50, 1 ♀ (TU 2001); *Tangipahoa:* Lee Landing, IX-6-50, 1 ♂, 1 ♀ (TU 2181); Ponchatoula, IX-6-50, 1 ♂ (TU 2182); *Union:* Haile, VI-20-50, 1 ♂ (TU 2067).

POLITES VIBEX BRETTUS (BOISDUVAL AND LECONTE), the Whirlabout.—There is no apparent localization of this species in Louisiana, and although it is not common, it has been taken often in the pine flats of the Florida parishes and in other parts of the state. All specimens were collected while they were feeding on wild flowers. The larvae feed on grasses.

P. vibex brettus has not been recorded from Louisiana previously. The records are: *Evangeline:* 12 miles west of Mamou, X-16-49, 1 ♀ (TU 1576); *Sabine:* Negreet, VI-7-50, 2 ♂♂, 2 ♀♀ (TU 2101); 8 miles west of Negreet, VII-8-50, 1 ♂ (TU 2107); *St. Tammany:* Covington, IX-8-50, 1 ♂ (TU 2180) and IX-8-50, 3 ♂♂ (TU 2196); *Tangipahoa:* Robert, IX-6-50, 2 ♂♂ (TU 2185); *Union:* Haile, VI-20-50, 1 ♀ (TU 2067).

WALLENGRENIA OTHO OTHO (J. E. SMITH), Otho's Skipper.—Thus far in Louisiana this species has been collected mostly in the Florida parishes. The larvae feed on crab grass (*Panicum sanguinale*) according to Klots (1951).

Otho's skipper has not been recorded from Louisiana previously. The records are: *Orleans:* New Orleans, III-22-50, 1 ♂ (TU 1821); *St. Tammany:* Covington, 4 ♂♂, 2 ♀♀ (TU 2196); *Tangipahoa:* Ponchatoula, IX-6-50, 1 ♂ (TU 2182).

POANES VIATOR (EDWARDS), the Broadwinged Skipper.—Although this species apparently is locally very common in Louisiana during the spring and early summer months, only twelve specimens have been collected thus far. All of these were taken together while they were feeding on a roadside strip of daisies. The flight is exceptionally fast. Lindsey, Bell and Williams (1931) stated that the species flies from June to August. Nothing is known of the early stages.

The Louisiana record is: *St. Charles:* Norco, III-10-51, 6 ♂♂, 6 ♀♀ (TU 2301). Previously it had been recorded from Orleans parish by Scudder (1889).

ATRYTONE AROGOS AROGOS (BOISDUVAL AND LECONTE), the Iowa Skipper.—A single specimen has been collected in Louisiana while it was feeding on daisies growing in a garbage dump. Little information is available on the immature stages.

The species has not been recorded from Louisiana previously. The lone record is: *St. Tammany:* Covington, IX-8-50, 1 ♂ (TU 2197).

ATRYTONE DUKESI LINDSEY, Dukes' Skipper.—A single specimen has been taken in Louisiana. The species was described from Mobile, Alabama, and Holland (1931) predicted that it would occur over a wider area along the Gulf, although Klots (1951) made no mention of it west of Alabama. The Louisiana record constitutes a possible westward range extension. Information is lacking concerning the early stages.

The species has not been recorded from Louisiana previously. The lone record is: *West Carroll:* 11½ miles west of Oak Grove, VI-19-50, 1 ♂ (TU 2064).

ATRYTONE RURICOLA METACOMET (HARRIS).—The Dun Skipper apparently is not common in Louisiana, as only two specimens have been taken, and those were in the western and northern part of the state. Almost nothing is known about the immature stages of this skipper.

A. ruricola metacomet has not been recorded from Louisiana previously. The records are: *Sabine:* Negreet, VII-7-50, 1 ♂ (TU 2101); *Union:* Marion, VI-24-50, 1 ♂ (TU 2075).

OLIGORIA MACULATA (EDWARDS), the Twin Spot.—Edwards (1865) described this species from New Orleans, but both Holland (1931) and Lindsey, Bell and Williams (1931) considered it to be most abundant toward the Carolinas. Klots (1951) stated that it strays west to Texas. Indeed, the few specimens collected in Louisiana have all been taken from the eastern part of the state, particularly in the pine flats of the Florida parishes. Very little is known concerning the immature stages, although the larvae presumably feed on grass (Klots, 1951).

The records are: *St. Tammany:* St. Tammany, IV-13-50, 1 ♀ (TU 1903); Covington, IX-8-50, 1 ♂ (TU 2196); Hickory, IX-13-50, 1 ♂ (TU 2198); *Tangipahoa:* Ponchatoula, IX-6-50, 2 ♂♂ (TU 2182).

LEREMA ACCIUS (J. E. SMITH).—The Accius Skipper apparently is not abundant in Louisiana. Thus far it has been taken during the late summer months only, although it has been reported to fly during all months of the year in the southernmost limits of its range (Lindsey, Bell and Williams, 1931). The larvae feed on grasses and Indian corn according to Klots (1951).

The records are: *Pointe Coupee:* McCrea, X-14-49, 1 ♂, 1 ♀ (TU 1567, 1568); *St. Tammany:* Covington, IX-5-50, 1 ♀ (TU 2180) and IX-8-50, 3 ♂♂, 1 ♀ (TU 2196); Folsom, IX-7-50, 1 ♂ (TU 2187); *Tangipahoa:* Ponchatoula, IX-6-50, 1 ♂ (TU 2182). Previously it had been recorded from Madison (Glick, 1939) and Orleans parishes (Edwards, 1865).

AMBLYSCIRTES VIALIS (EDWARDS).—A single specimen of the Roadside Skipper has been taken in Louisiana. Klots (1951) stated that the range is from southern Canada to Florida, and westward to Texas, but Holland (1931) wrote that it was common in the Mississippi valley. Lindsey, Bell and Williams (1931) stated that *vialis* apparently is replaced by another species in the southeastern states. There can be no doubt, however, that *vialis* is an occasional visitor in Louisiana, particularly in the northern parishes. The caterpillars feed on grasses.

A. vialis has not been recorded from Louisiana previously. The record is: *Webster:* Leton, VIII-6-49, 1 ♂ (TU 1449).

AMBLYSCIRTES TEXTOR (HUBNER).—The Wovenwinged Skipper is represented in Louisiana by a single specimen. This individual was taken while it was feeding on a blackberry flower. Nothing is known of the immature stages.

A. textor has not been recorded from Louisiana previously. The record is: *Jefferson:* Kenner, III-9-51, 1 ♂ (TU 2297).

LERODEA L'HERMINIERI (LATREILLE), the Fuscous Skipper.—Five specimens of this uncommon skipper have been taken in Louisiana during the summer months. Little is known about the immature stages.

L. l'herminieri has not been recorded from Louisiana previously. The records are: *St. Helena:* Liverpool, IX-7-50, 1 ♂ (TU 2193); *Tangipahoa:* Ponchatoula, IX-6-50, 3 ♂ ♂ (TU 2182); *Union:* Haile, VI-20-50, 1 ♂ (TU 2066).

LERODEA EUFALA (EDWARDS), the Eufala Skipper.—This species also is rare in Louisiana. Only four specimens have been taken in the state and these in late summer and early autumn. The larvae feed on grasses.

The records are: *St. Bernard:* Shell Beach, X-18-49, 2 ♂ ♂, 1 ♀ (TU 1595); *Tangipahoa:* Lee Landing, IX-6-50, 1 ♀ (TU 2182). Previously it had been recorded from Madison parish by Glick (1939).

CALPODES ETHLIUS (STOLL), the Brazilian Skipper.—Although this species apparently is common in Louisiana, only one specimen has been taken during the survey. The flight is very rapid, the skipper rising and falling in a very quick undulating manner.

Jung (1950) reported large numbers of the larvae on canna in New Orleans, and the single adult specimen in the Tulane collection was reared from a pupa found on canna leaves. Dr. Forbes informed the writer (in correspondence) that he observed numerous larvae and adults of *ethlius* in New Orleans on January 1, 1933.

The single record is: *Orleans:* New Orleans, X-17-50, 1 ♀ (TU 2224).

PANOQUINA PANOQUIN (SCUDDER).—The Salt-marsh Skipper has not been taken by the writer in Louisiana, but is included here on the basis of Scudder's (1889) report of it from New Orleans. Nothing is known about the early stages.

PANOQUINA OCOLA (EDWARDS).—The Ocola Skipper is fairly common in Louisiana during the late summer, frequenting the edges of forested areas. Nothing is known about the immature stages.

P. ocala has not been recorded from Louisiana previously. The records are: *Allen:* Oberlin, X-16-49, 1 ♀ (TU 1574); Hampton, X-16-49, 1 ♂ (TU 1579); *Evangeline:* St. Landry, X-14-49, 1 ♀ (TU 1569); Point Blue, X-16-49, 1 ♂ (TU 1579); *Pointe Coupee:* McCrea, X-14-49, 1 ♂, 1 ♀ (TU 1567, 1568); *St. Bernard:* Delacroix Island, X-18-49, 1 ♂ (TU 1592); *St. Charles:* Norco, I-24-50, 1 ♂ (TU 1763); *St. Tammany:* Folsom, IX-7-50, 1 ♀ (TU 2187); *Tangipahoa:* Ponchatoula, IX-6-50, 2 ♂ ♂, 1 ♀ (TU 2182).

Summary

Butterflies and skippers were collected in Louisiana during three years (1948-1951) and these records are coupled with those of other institutional and published records to form a composite list for the state. Before the writer's survey was begun there had been 43 species recorded, and during its progress a local study by Jung (1950) added 17 new state records, bringing the total to 60 by July 1950. With the completion of the present study 38 previously unrecorded species are added, and the state list now totals 98.

An attempt was made to collect in many areas of the state, and during different times of the year. Fifty of the 64 parishes of Louisiana were sampled, and two additional ones are included in the literature. Best represented are the southeastern parishes, New Orleans and vicinity. A total of 1501 adult butterflies and skippers were examined in the course of the study.

Each species on record is listed with observations by the writer and a summary of the collection data arranged by parishes.

From laboratory analyses of the records certain geographic patterns are noted. While most species are found distributed more-or-less evenly throughout the state, some are restricted to particular physiographic or vegetational regions. *Euptychia areolata areolata, E. gemma gemma, Celastrina argiolus pseudargiolus, Eurema daira daira, Wallengrenia otho otho* and *Oligoria maculata* appear to inhabit only the Florida Parish pine area, with *E. gemma gemma* occasionally visiting the Upland pine areas. *Euptychia cymela cymela, Anaea andria, Graphium marcellus marcellus* and *Anthocharis genutia* are more-or-less restricted to upland pine and hardwood areas. *Heliconius charitonius, Agraulis vanillae nigrior, Euptoieta claudia claudia* and *Papilio cresphontes cresphontes* are restricted almost entirely to the southern parishes.

An analysis of the flying dates leads to the general conclusion that most of the common species fly almost throughout the year in Louisiana, with their peaks of abundance in the hot summer months. Figure 3 summarizes the seasonal distribution of all of the commoner species.

On comparison with published distribution patterns it appears that the Louisiana specimens of *Melitaea nycteis nycteis* constitute a range extension of significance. Since the species is not abundant in Louisiana this must be the southern tip of its range. The collections of *Polites manataaqua manataaqua, Hemiargus isolus* and *Atrytone dukesi* assist in defining the ranges of these species.

The 98 species recorded here are not all of the butterflies and skippers expected from the state. More concentrated sampling over a longer period of the year, and a more intense consideration of the immature stages will undoubtedly reveal a greater number of species. Perhaps in due time the writer may be able to fill in the vacancies, however, it is hoped that this paper will stimulate entomologists to initiate further studies of the Lepidoptera of Louisiana.

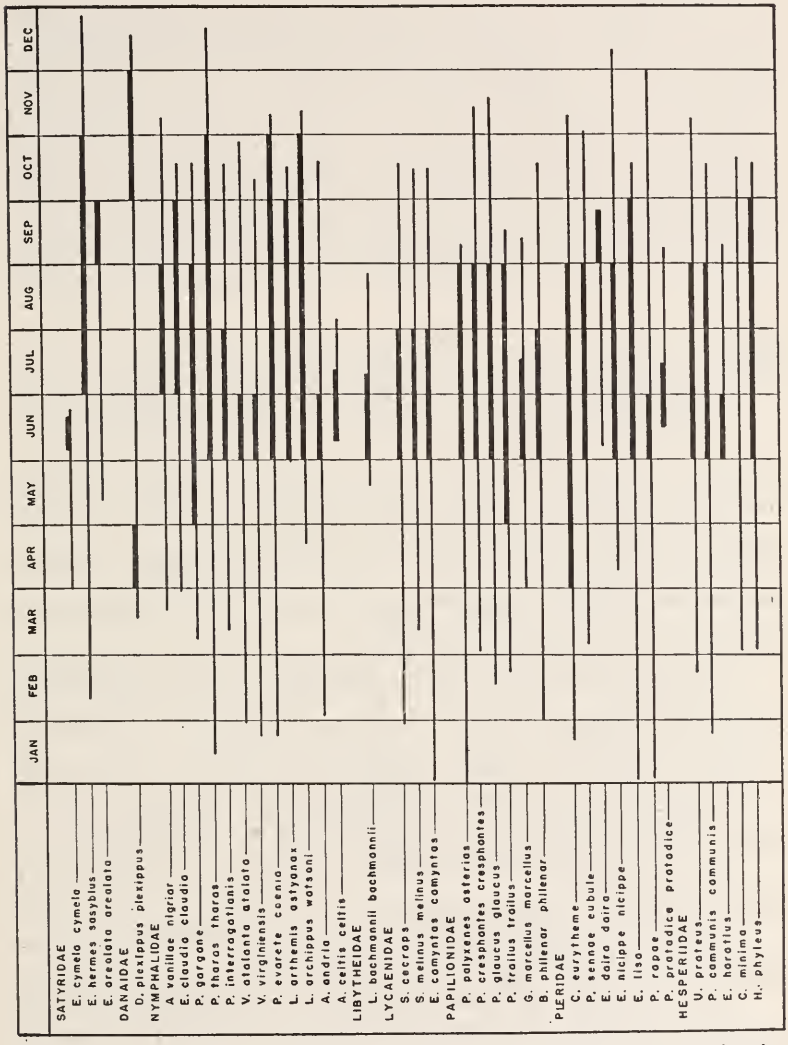


Figure 3. Summary of flying seasons of the commoner species in Louisiana; thickened parts of bars indicate months of greatest abundance.

Acknowledgements

The writer wishes to express his thanks and sincere appreciation to Dr. George H. Penn, Tulane University, without whose encouragement this research could not have been completed. Thanks are due to Dr. E. S. Hathaway, Tulane, for the interest he showed during this study, and to Dr. Ralph L. Chermock, University of Alabama,

who so willingly identified the specimens sent to him for confirmation, and who criticized the preliminary and final drafts of the manuscript. Appreciation is due to Dr. George H. Bick, Tulane, for helpful suggestions and for collections from the Delta region. The writer is indebted to Dr. Fred R. Cagle, Tulane, for invitations extended to accompany him in the field. Dr. Lewis T. Graham kindly placed the collections of Southwestern Louisiana Institute at the writer's disposal. Invaluable aid was rendered by Dr. W. T. M. Forbes, Cornell University, and by Dr. Austin H. Clark, U. S. National Museum, both of whom carefully criticized the manuscript. Also, to his wife who spent many hours preparing the final draft the writer will be ever grateful.

References Cited

Beall, Geoffrey 1946. Seasonal variation in sex proportions and wing length in the migrant butterfly, *Danaus plexippus* L. 3. Migrants of the autumn in Louisiana. *Trans. Royal Ent. Soc. London,* 97: 342-343.

---------- 1948. The fat content of a butterfly, *Danaus plexippus* Linn., as affected by migration. *Ecology,* 27: 80-94.

Chermock, Ralph L. 1947. A new subspecies of *Limenitis archippus. Amer. Mus. Novitates,* No. 1365: 1-2.

Clark, Austin *H.* 1941. Notes on some North and Middle American danaid butterflies. *Proc. U. S. Nat. Mus.,* 90: 531-542.

[Comstock, John H.] 1882. The hog caterpillar of the orange. *Rept. U. S. Comm. Agric.,* 1881: 246-248.

Comstock, William P. and F. Martin Brown 1950. Geographical variation and subspeciation in *Heliconius charitonius* Linnaeus. *Amer. Mus. Novitates,* No. 1467: 1-21.

Dos Passos, Cyril F. 1938. A new race of *Basilarchia archippus* Cramer from Louisiana. *Canad. Ent.,* 70: 243.

Edwards, William H. 1865. Description of certain species of diurnal Lepidoptera found within the limits of the United States and British America. *Proc. Ent. Soc. Phila.,* 4: 201-204.

Field, William D. 1941. Additional notes on *Calycopis cecrops* (Fabricius) and *Calycopis beon* (Cramer). *Jour. Kans. Ent. Soc.,* 14: 66-69.

Floyd, Ernest H. 1941. Investigations on the biology and control of the alfalfa caterpillar, *Colias eurytheme* Boisduval. *La. Agric. Exp. Sta., Louisiana Bull.,* No. 323: 16-25.

Gerould, John H. 1946. Hybridization and female albinism in *Colias philodice* and *Colias eurytheme.* A New Hampshire survey in 1943 with subsequent data. *Ann. Ent. Soc. Amer.,* 39: 383-397.

Glick, P. A. 1939. The distribution of insects, spiders, and mites in the air. *U. S. Dept. Agric., Tech. Bull.,* No. 673: 1-150.

Hine, James A. 1904. A contribution to the entomology of the region of the Gulf Biologic Station. *Gulf Biol. Sta. Bull.,* No. 2: 65-68.

---------- 1906. A second contribution to the entomology of the region of the Gulf Biologic Station. *Gulf Biol. Sta. Bull.,* No. 6: 65-83.

Holland, William J. 1931. *The Butterfly Book,* revised edition. New York: Doubleday and Co., pp. 1-424.

HOVANITZ, WILLIAM 1943. The nomenclature of the *Colias chrysotheme* complex in North America. *Amer. Mus. Novitates*, No. 1240: 1-4.

---------- 1944. The ecological significance of the color phases of *Colias chrysotheme* in North America. *Ecology*, 25: 45-60.

HOWARD, L. O. 1895. The gray hair-streak butterfly and its damage to beans (*Uranotes melinus* Hubn.). *Insect Life*, 7:354-355.

JOHNSON, FRANK and WILLIAM P. COMSTOCK 1941. *Anaea* of the Antilles and their continental relationships, with descriptions of new species, subspecies and forms. *Jour. N. Y. Ent. Soc.*, 49: 301-343.

JOHNSON, LAWRENCE 1886. [Communication]. *Proc. Ent. Soc. Wash.*, 1: 34-35.

JUDD, W. W. 1950. An assemblage of monarch butterflies (*Danaus p. plexippus*) on the north shore of Lake Erie. *Jour. N. Y. Ent. Soc.*, 58: 169-172.

JUNG, RODNEY C. 1939. On the occurrence of some of southern Louisiana's more common butterflies. *Tulane Biol.*, 3: 17-18. (mimeographed).

---------- 1950. An annotated list of the Lepidoptera of the New Orleans area. *Proc. La. Acad. Sci.*, 8: 42-48.

KLOTS, ALEXANDER B. 1951. *A Field Guide to the Butterflies of North America, East of the Great Plains.* Boston: Houghton Mifflin Co., pp. 1-349.

KOPMAN, HENRY H. 1903. The butterflies of Louisiana. *New Orleans Times Democrat*, April 12, 1903.

LINDSEY, A. W., E. L. BELL and R. C. WILLIAMS 1931. The Hesperoidea of North America. *Denison Univ. Bull., Jour. Sci. Laboratories*, 26: 1-142.

MCDUNNOUGH, J. 1938. Checklist of the Lepidoptera of Canada and the United States of America, Parts I and II. *Mem. So. Calif. Acad. Sci.*, 1: 1-272.

MORRIS, JOHN G. 1862. Synopsis of the described Lepidoptera of North America. *Smithson. Misc. Collections*, 4: 1-358.

MICHENER, C. D. 1947. A review of the subspecies of *Agraulis vanillae L. Amer. Mus. Novitates*, No. 1215: 1-7.

MONTGOMERY, ROBERT W. 1932. Records of Louisiana butterflies. *Ent. News*, 43: 182.

NIELSEN, ERIK T. and ASTRID T. NIELSEN 1950. Contributions toward the knowledge of the migrations of butterflies. *Amer. Mus. Novitates*, No. 1471: 1-29.

PARK, ORLANDO 1948. Observations on the migrations of monarch butterflies through Evanston, Illinois in September, 1948. *Chicago Acad. Sci., Nat. Hist. Misc.*, No. 30: 1-8.

[RILEY, C. V. and L. O. HOWARD] 1895. A new food plant for *Papilio turnus. Insect Life*, 6:40.

ROTHSCHILD, WALTER and KARL JORDAN 1906. A revision of the American Papilios. *Novitates Zool.*, 13: 411-752.

SAUNDERS, WILLIAM 1871. On the swarming of *Danaus archippus. Canad. Ent.*, 3:156-157.

SAVERNER, P. A. 1908. Migrating butterflies. *Ent. News*, 19: 218-220.

SCUDDER, SAMUEL H. 1889. *The Butterflies of the Eastern United States and Canada with Special Reference to New England.* Cambridge: published by the author; vols. I-III.

SHUFELDT, R. W. 1884. Observations upon a collection of insects in the vicinity of New Orleans, La., during the years 1882 and 1883. *Proc. U. S. Nat. Mus.*, 7: 331-338.

SKINNER, HENRY 1897. A new species of *Debis*. *Ent. News*, 8: 236.

_____ 1907. Studies of *Thecla irus* Godart and *Thecla henrici* Grote and Robinson. *Ent. News*, 18: 129-132.

VIOSCA, PERCY JR. 1933. *Louisiana Out-of-Doors.* New Orleans: published by the author, pp. 1-187.

von REIZENSTEIN, LUDWIG 1863. *Catalogue of the Lepidoptera of New Orleans and its Vicinity.* New Orleans: Isaac T. Hinton, pp. 1-8.

WILLIAMS, C. B. 1930. *The Migration of Butterflies.* Edinburgh: Oliver and Boyd, Biol. Monogr. and Manuals, No. 9.

_____ 1937. Butterfly travelers. *Nat. Geogr. Mag.*, 71: 568-585.

LIBRARY
MAR - 3 1961
HARVARD UNIVERSITY

TULANE STUDIES IN ZOOLOGY

Volume 1, Number 11 August 26, 1954

TWO NEW SPECIES OF THE GENUS *GRAPTEMYS*

FRED R. CAGLE,
DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY, NEW ORLEANS.

TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico and the Caribbean Sea. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

HOBART M. SMITH, Professor of Zoology, University of Illinois, Urbana, Illinois.

ARCHIE F. CARR, JR., Professor of Biological Sciences, University of Florida, Gainesville, Florida.

T. PAUL MASLIN, Associate Professor of Biology, University of Colorado, Boulder, Colorado.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

When citing this series authors are requested to use the following abbreviations: *Tulane Stud. Zool.*

Price for this number: $0.75.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University,
New Orleans, U. S. A.

Assistants to the Editor:
Carol L. Freret
Robert E. Gordon

HARVARD UNIVERSITY

TWO NEW SPECIES OF THE GENUS *GRAPTEMYS*

FRED R. CAGLE,
Department of Zoology, Tulane University, New Orleans.

Two distinctive, undescribed populations of turtles were found in Mississippi and Alabama by the Tulane University field crews of 1952 and 1953. The turtles are abundant at the type localities and are the dominant species of turtles present.

Both species are closely related to *Graptemys oculifera* (Baur) and with this species form a unique complex of three allopatric species ranging from the Pearl River in the west to the Alabama river in the east. The three groups of populations are recognized as species because: (a) the degree of difference between the three groups is much greater than that between the subspecies of related species occurring in the central United States; (b) the degree of difference is as great as that occurring between sympatric species of this and related genera; (c) there are no intermediates. These factors suggest that these populations have been reproductively isolated for a long period. It is not possible to conclude that these three forms would not be capable of interbreeding if they were not spatially isolated.

The following abbreviations are used in the descriptions: Cl., carapace length (not along curve); Cw., carapace width; Pl., plastron length; Pw., plastron width; Hw., head width; Ht., height; Aw., alveolar width. All measurements are maximum. The size of individuals is expressed as plastron length.

UMMZ = University of Michigan Museum of Zoology; CNHM = Chicago Natural History Museum.

The illustrations in color were provided through the cooperation of Roger and Isabelle Hunt Conant who had photographed the turtles for inclusion upon one of the color plates in their forthcoming *Field Guide to the Reptiles and Amphibians*. Mr. George P. Meade generously provided the funds for their publication here. The research was aided by a grant from the National Science Foundation.

The collections essential to these descriptions could not have been made without the enthusiastic field work of graduate students. I am especially grateful to A. H. Chaney, Robert Gordon, Donald Tinkle, Robert Webb, Walter Stone, and Howard Suzuki.

GRAPTEMYS FLAVIMACULATA, sp. nov.
Yellow-blotched Sawback

Holotype.—Tulane 14798, a juvenile male, collected from the Pascagoula River, 13 miles S.W. of Lucedale, George Co., Mississippi, 18 Aug. 1952 (figs. 3, 5, 7).

Paratypes.—Tulane 14752, 14754, 14756-766, 14768, 14772, 14774-776, 14778-785, 14788, 14790, 14795, 14799-802, 14804, 14806-809, 14811-812, 14815, 14818, 14821-822, 14825-827, 14829, 14832-833, 14842, 14845-846, 14850, 14852-854, 14857-858, 14862-863, 14865-

871, 14873-875, 14920-921, 14935, 14938; CNHM 69806-808; UMMZ 108567-571, 36 juveniles, 44 males and 3 females collected at the type locality by a Tulane University field crew.

Hypodigm.—A total of 124 preserved specimens, 74 examined by dissection and not retained, and many others observed in the field provided a series of observations for the analysis of variation of this species. The study of these individuals has also provided a basis for determination of some aspects of the behavior and for estimating the population structure.

Diagnosis.—*Graptemys flavimaculata* is a member of a narrow-head complex that includes three species occurring only in Louisiana, Mississippi and Alabama, *Graptemys oculifera* in the Pearl River drainage, *Graptemys flavimaculata* in the Pascagoula River and its tributaries, *Graptemys nigrinoda* in the Black Warrior and Alabama Rivers (fig. 9).

G. flavimaculata differs from *G. nigrinoda* in that: the postorbital mark is rectangular or triangular, is broader than any of the lateral neck lines entering the orbit, and is usually joined to a longitudinal line; the ventral surface of the jaw is dominated by broad yellow lines much wider than the olive-green interspaces; each costal with a large yellow or orange central blotch or crescent; the vertebral spines are high, narrow, laterally compressed; the edge of the carapace of males and juveniles is much less serrate (Table 1).

G. flavimaculata differs from *G. oculifera* in that: the orbital mark is broad and is ordinarily joined to a dorsal longitudinal neck line; the lower jaw is dominated by broad yellow lines; each costal has a large blotch or crescent of yellow.

Description of holotype—Carapace length, 8.05 cm; carapace width at juncture of fourth and fifth marginals, 6.15 cm; carapace width at juncture of seventh and eighth marginals, 6.72 cm; plastron length, 7.43 cm; width of posterior lobe of plastron, 3.63 cm; height (measured in vertical line through spine of second vertebral), 3.70 cm; height at spine of third vertebral, 3.41 cm; head width (measured at anterior edge of tympanum) 1.24 cm; length of symphysis of lower jaw, 0.44 cm; alveolar width of upper jaw, 0.25 cm.

Edge of carapace serrate; each marginal projecting beyond anterior corner of the next posterior one. Each marginal with a wide, yellow bar or semicircle of yellow. Each costal with a broad ring or yellow blotch (figs. 1, 3).

Plane of the plastron 1.40 cm below a plane through the edge of the fifth to the seventh marginals. Yellow color predominant on the plastron, bridge and ventral surface of marginals. Black plastral marks extending along the sutures between each pair of shields (fig. 7).

Neck with 19 longitudinal, yellow lines; those on the ventral surface twice the width of those on the dorsal surface. Longitudinal, interorbital line nearly as wide as widest dorsal neck lines and terminating above postorbital mark. Three yellow lines between the orbits. Two broad, yellow lines entering the orbit below a triangular post-

TABLE 1
A COMPARISON OF *Graptemys oculifera, flavimaculata* and *nigrinoda*

	oculifera	*flavimaculata*	*nigrinoda*
Carapace margin of adult ♂♂	slightly serrate	slightly serrate	very serrate
Vertebral projection	laterally compressed; spine-like	laterally compressed; spine-like	broad, rounded knob-like
Postorbital mark	Ovoid, rectangular or rounded; usually not connected with dorsal, longitudinal line; usually not wider than widest neck line	usually rectangular and joined to a dorsal, longitudinal neck line; usually 2 or 3 times wider than widest neck line	a vertical curved bar not wider than neck lines; connected dorsally by diagonal lines to form a Y shaped mark
Neck lines entering orbit	two broad, yellow lines; width equal to width of black area between them	two to four yellow lines; 2 widest much broader than width of olive-green area between them	usually four yellow lines; 2 widest about twice width of narrower lines
Interorbital line	broad; equal to or greater than width of broadest neck lines	narrower than neck lines	narrower than neck lines
Color background of soft parts	black	olive-green	black
Markings, lower jaw	longitudinal yellow lines as wide as black interspaces; black color predominant	longitudinal yellow lines much wider than olive-green interspaces; yellow color predominant	longitudinal lines as wide as interspaces; black color predominant
Markings, forelegs	lines from 2nd and 4th digits equal in width; no or very narrow lines from base of 3rd digit	lines from base of 2nd and 4th digits very broad; line from base of 3rd digit ⅓ to ½ width of line from 3rd digit	as in *oculifera*
Markings, costal shields	yellow or orange circle formed on each costal by a broad line (broader than widest neck line)	large yellow blotch or crescentic mark covering most of the surface	yellow or orange semi-circle or circle formed by a narrow line (much narrower than widest neck line
Color, plastron	yellow or orange	light cream	yellow often tinted with red

orbital mark (figs. 1, 5).

Horny edges of both upper and lower jaws light in color. Ventral surface of lower jaw with two broad, transverse, yellow bands.

Anterior surface of forelegs with wide, yellow lines; those from the base of second and fourth toes are the broadest.

Description of paratypes.—The paratypic series is divided into juveniles, adult males and adult females to insure adequate description.

Juveniles.—The juveniles represent individuals in the first to the tenth seasons of growth (figs. 11, 13). The color pattern of the individuals greater than 9 cm in plastron length is basically the same as that of the smaller juveniles but the contrast between the yellow or orange markings and the background is less.

The head pattern in lateral view consists of two wide, yellow lines extending posteriorly from the orbit along the neck, a triangular or vertically elongated postorbital mark, and a broad yellow line extending the length of the lower jaw. The postorbital mark is, in most individuals, joined to a longitudinal line on the dorsal surface of the head (figs. 1, 11, 13).

The head pattern from the dorsal view consists of a wide yellow line between the orbits extending from a point just above the nostrils to above the center of the postorbital mark; two lines from the upper edge of the orbit that, in most individuals, join the postorbital mark and continue posteriorly onto the neck. The latter lines are interrupted in some individuals. The background color is black (figs. 11, 13, 15).

The lower jaw is dominated by wide yellow lines broadly bordered with black. Of the three or four transverse yellow lines, the most posterior ones join longitudinal lines (figs. 11, 13, 15). The neck has 17-20 wide yellow lines around its circumference at the rear of the skull.

The carapace has bright yellow or orange central splotches on each costal. These are extremely variable in shape but usually cover more than one-third the total area of each shield. In some individuals (14795) they are rounded, in others (14788) they are crescent-like. The upper surface of each marginal has a semicircle of yellow enclosing a darker area having a faint indication of two concentric light lines. Each of the vertebral spines is conspicuously colored black.

The plastron has a pattern of black lines tending to extend along the seams. The background is cream or light.

The anterior surface of the forelimbs has fine yellow lines on a black background. Those extending from the base of the second and fourth toes are the wider.

The jaws have a thin, sharp-edged horny covering. That of the upper overlaps the lower to provide a scissor-like action. The alveolar surfaces are not broadened in the larger turtles, Hw/Aw = 4.7-5.8; no correlation with size.

The head is narrower in relation to plastron length in the larger juveniles. Pl/Hw = 4.1-4.5 in those 5.0 cm to 5.3 cm in plastron

length; 5.5-6.6 in the larger turtles.

The carapace width decreases in proportion to plastron length in the larger individuals; Pl/Cw = 0.91-0.99 in those 5.0 cm to 5.5 cm in plastron length, 0.95-1.1 in the larger ones. The height is reduced in larger turtles; Pl/Ht = 1.7-1.9 in those 5.0 cm to 5.5 cm in plastron length; 1.8-2.1 in the larger ones.

The spines of the first four vertebrals are conspicuous in all the juveniles (fig. 11). In those with a plastron length of less than 11 cm the height of the spines of the second vertebral is 2/3 to 3/4 the length of the seam between the second and third marginal. The elevations on the first and fourth vertebrals are ridge-like, those of the second and third are distinct spines.

Adult males.—The adult* males in the paratypic series range from 7.10 cm to 9.5 cm in plastron length. The smaller adult males (less than 8 cm in plastron length) have the same color pattern as the juveniles. The larger males (more than 8 cm in plastron length) lose the orange tint in the blotches of the carapace and the lines of the head. The plastral pattern is lightened and poorly defined in the larger individuals.

The spines of the vertebral shields are slightly lower in the large males than in the juveniles and those of the first and third shields are rounded (14850, 14858). The carapace edge of the largest male is less serrate anteriorly than in smaller males; the posterior lateral corners of the fifth and sixth marginals project but slightly beyond the anterior lateral corner of the next posterior marginal (fig. 15).

The height is not reduced with increased length as it is in other species, Pl/Ht = 1.9-2.2. The carapace is somewhat narrowed as the male increases in length; Pl/Cw = 1.0-1.1.

The head is slightly narrower in relation to plastron length in larger males, Pl/Hw = 5.6-5.8 in those 7-8 cm in plastron length; Pl/Hw = 6.0-6.3 in those greater than 8 cm in length. There is no consistent broadening of the alveolar surfaces in larger males, Hw/Aw = 5.1-6.1.

The third claw of the forefoot is slightly longer than the length of the seam between the second and third marginals.

Adult females.—The adult females retain the color pattern of the juveniles but the blotches on the carapace and the black lines of the plastron are not as distinct. The largest female (14815) has the black background of the carapace lightened by the development of irregular areas of olive-green. The black borders of the yellow marks on the marginals are indistinct. The only remaining vestige of the black lines of the plastron are present on the gular, humeral and anal shields.

The spines of the vertebral shields are much more reduced than in adult males but remain clearly evident on the first four vertebrals (height of spine of second vertebral = 1/4-1/3 length of seam between first and second marginals). The carapace edge is not serrate except between the eighth to the twelfth marginals.

The smallest mature female (14920) in the paratypic series has the following measurements: Pl. 14.0, Cl. 14.9, Cw. 13.0, Ht. 6.5, Hw. 2.1, Aw. 0.43. The largest (14815) has these measurements: Pl. 15.9, Cl. 17.4, Cw. 14.3, Ht. 7.3, Hw. 2.33, Aw. 0.52.

The carapace height is not reduced in comparison with the juveniles and adult males, Pl/Ht = 1.9-2.2. The carapace is slightly broadened in contrast with the adult males, Pl/Cw = 1.1 (in all three individuals).

The head is proportionately broader than in adult males, Pl/Hw = 4.5-4.9 and the alveolar surfaces are wider, Hw/Aw = 4.5-4.9. The third claw of the forefoot is 1/2 to 2/3 the length of the seam between the second and the third marginal.

Range.—Specimens are available from three localities; the type locality, the Chickasawhay River and 15 miles from the mouth of the Pascagoula River, Jackson County, Mississippi (AMNH 46774, collected by M. J. Allen, 1930). All specimens have been taken from the Pascagoula River or its tributaries. It is apparent that this species is restricted to this stream system as repeated efforts to collect it from adjacent rivers to the east and west were unsuccessful (fig. 9). Populations undoubtedly occur in all the major tributaries and should be especially abundant in the Escatawpa River.

Habitat.—The Pascagoula River basin, comprising 8,900 square miles, has had the greatest concentration of industry in Mississippi. Two of the tributaries, Tallahala and Sowashee Creeks, have been highly polluted by sewage and waste from wood pulp and chemical industries (Anderson, 1950). This pollution has apparently had no tendency to reduce the *Graptemys* populations and has probably, through contributing to the increase of the mollusc populations, improved the general habitat for *G. flavimaculata.*

The river at the type locality has a sand and clay bottom and many sand bars and beaches. Flood-stranded debris is abundant and much of the shoreline has a stand of dense brush. The debris and brush extending into the water provides shelter for turtles. The river is 75 to 250 feet in width and deep pools are separated by long stretches of shallow water. A moderately rapid current maintains a narrow channel through the shallow areas.

These turtles were most abundant about the tangled roots of trees. Often several turtles were observed lying together in such places. The approach of the boat usually caused them to leave the resting site and swim rapidly toward deep water.

The Chickasawhay River is 30-150 feet wide; the banks have exposed areas of limestone in many places and the bottom is generally rock and sand. Deep, quiet pools are connected by fast-flowing stretches of shallow water. Drift wood and rocks are abundant along the shores. No *G. flavimaculata* were taken in the faster current or the static water but they were abundant in the snags in the slower current.

This species occurs with *Graptemys pulchra, Pseudemys floridana*

mobilensis, Pseudemys scripta elegans and *Sternotherus carinatus.* It is clearly the dominant turtle species in the Pascagoula and Chickasawhay Rivers.

Bionomics.—*G. flavimaculata* is a comparatively small, rapidly growing turtle adapted to live in moderate current. The smallest sexually mature male studied had a plastron length of 6.67 cm; the smallest mature female had a plastron length of 13.30 cm.

The males may reach sexual maturity in the second growing season. The smallest mature male was in its second growing season when collected and three others ranging in size from 7.47 cm to 8.00 cm were in the third and fourth seasons. The largest male studied had a plastron length of 10.95 cm.

The age at maturity of females could not be determined as the early growth rings were not evident in any mature individual. None of the females larger than 14 cm in length had measurable growth zones.

GRAPTEMYS NIGRINODA, sp. nov.

Black-knobbed Sawback

Holotype.—Tulane 14662, a juvenile female, collected from the Black Warrior River, above Lock 9, 17.5 miles SSW of Tuscaloosa, Tuscaloosa County, Alabama (figs. 4, 6, 8).

Paratypes.—Tulane 14643, 14647-648, 14652-653, 14655-657, 14659, 14664-665, 14682, 14691, 14694, 14697, 14700, 14706, 14708-710, 14714, 14720, 14723, 14725, 14729; CNHM 69809-811, UMMZ 108572-574, 26 juveniles, 5 adult males.

Diagnosis.—*Graptemys nigrinoda* differs from *G. flavimaculata* and *G. oculifera* in that: the yellow postorbital mark is boomerang-shaped and is joined to the mark of the opposite side by a diagonal line; the interorbital line is narrow or indistinct; each costal has a circular or semicircular mark formed by a narrow yellow line; the vertebral spines are flattened, compressed, knob-like; the carapace is very serrate.

Hypodigm.—A total of 117 individuals were available for study from two localities and numerous others were observed in the field. The data derived from field observations and a study of the 117 preserved individuals provide the basis for the information presented.

Description of the holotype.—Maximum carapace length, 8.02 cm; carapace width at juncture of fourth and fifth marginals 6.54 cm; carapace width at juncture of seventh and eighth marginals 6.91 cm; maximum plastron length 7.52 cm; maximum width of posterior lobe of plastron, 3.87 cm; maximum height (measured in vertical line through spine of second vertebral, 3.42 cm; height at spine of third vertebral 3.30 cm; maximum head width (measured at anterior edge of tympanum) 1.32 cm; length of symphysis of lower jaw 0.57 cm; alveolar width of upper jaw 0.28 cm.

Edge of carapace very serrate (fig. 4). General color of carapace dark olive green. Faintly defined, narrow circular or semicircular mark formed by a thin yellow line on each marginal and costal (figs.

2, 4).

Plane of the plastron 1.23 cm below a plane through the edge of the fifth to the seventh marginals. Yellow color predominant on plastron and ventral surfaces of marginals. Branching, black pattern on plastron (fig. 8).

Neck with 25 longitudinal yellow lines; those on the ventral surface not much wider than those on the dorsal surface. Longitudinal interorbital line narrower than lateral neck lines. Fine yellow lines between orbits. Four yellow lines entering the orbit laterally; two of these broader than others. Postorbital mark boomerang-shaped and joined to mark of opposite side by a diagonal line (fig. 2).

Ventral surface of lower jaw with a broad, transverse yellow line (fig. 8).

Anterior surface of forelegs with five yellow lines.

Description of the paratypes.—The paratypic series is divided into two groups, juveniles and adult males.

Juveniles.—The juveniles are in their first or second season of growth. The background color of the carapace is dark olive green and that of the soft parts intense black.

The head pattern differs from that of juveniles of *flavimaculata* in that the postorbital yellow mark is a vertically elongated, boomerang-shaped line extending posteriorad on the dorsal surface to join the mark of the opposite side to form a **Y**. The interorbital, longitudinal stripe is narrow and indistinct in many individuals.

The lower jaw has one broad, yellow transverse line sometimes bordered both anteriorly and posteriorly by narrow yellow lines. Two of the wide, longitudinal neck lines join behind the level of the jaw juncture to form another transverse line. The lower surface of the neck is dominated by black on which the yellow lines appear to be superimposed (figs. 10, 12).

The carapace has a complete circle of a narrow yellow line on each costal. The knob-like vertebral spines are intense black. The upper surface of each marginal has a semicircular mark formed by a narrow yellow line. The ventral surface of each marginal may be yellow with an ocellus of black and yellow rings, or the yellow may be reduced to an irregular blotch on the medial side with the remainder of the marginal covered with alternating black and yellow lines (figs. 2, 8).

The plastron is yellow to bright orange with black lines extending along the seams (fig. 8). The anterior surface of the forelimb has two to five yellow lines. When four or five are present, those from the base of the second and fourth digits are much the wider.

The jaws are as described for *flavimaculata*. The alveolar width is contained 4.0-6.0 times in the head width. There is no relative broadening of the alveolar surface in the larger individuals.

The head is narrower in relation to plastron length in the larger turtles than in the smaller, Pl/Hw = 4.6-5.6. The carapace width decreases in proportion to plastron length with size, Pl/Cw = 0.9-1.0.

Figures 1-2. **1** (upper), *G. nigrinoda*, sp. nov.; **2** (lower), *G. flavimaculata*, sp. nov. (Photographs and color renditions by Isabelle Hunt Conant).

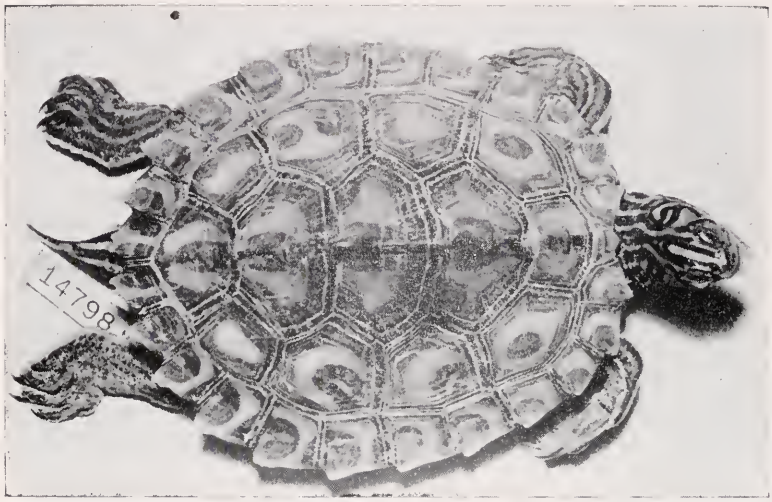


Figure 3. Dorsal view, *G. flavimaculata,* sp. nov. (Photograph by Isabelle Hunt Conant).

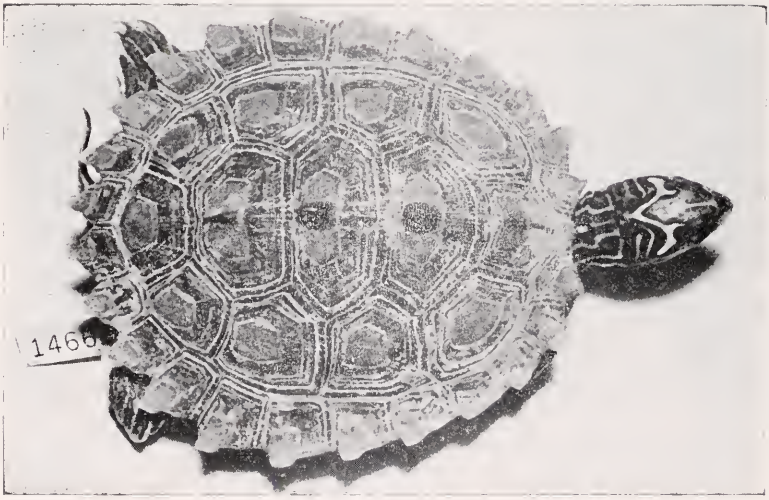


Figure 4. Dorsal view, *G. nigrinoda,* sp. nov. (Photograph by Isabelle Hunt Conant).

Figure 5. Lateral view, *G. flavimaculata*, sp. nov. (Photograph by Isabelle Hunt Conant).

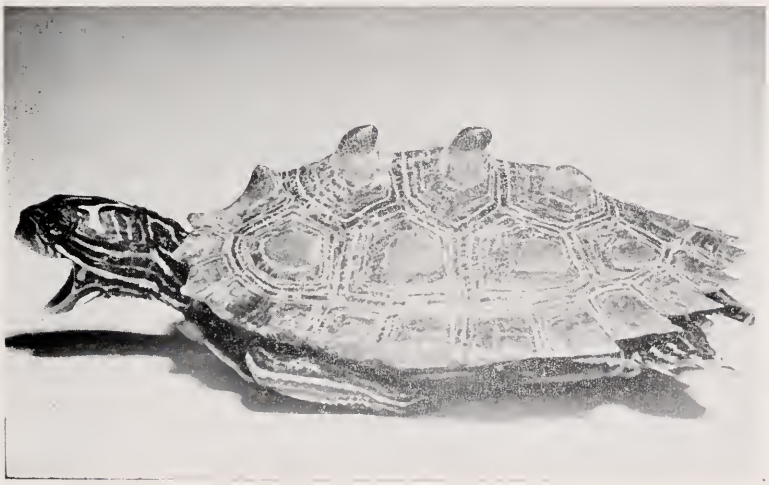


Figure 6. Lateral view, *G. nigrinoda*, sp. nov. (Photograph by Isabelle Hunt Conant).

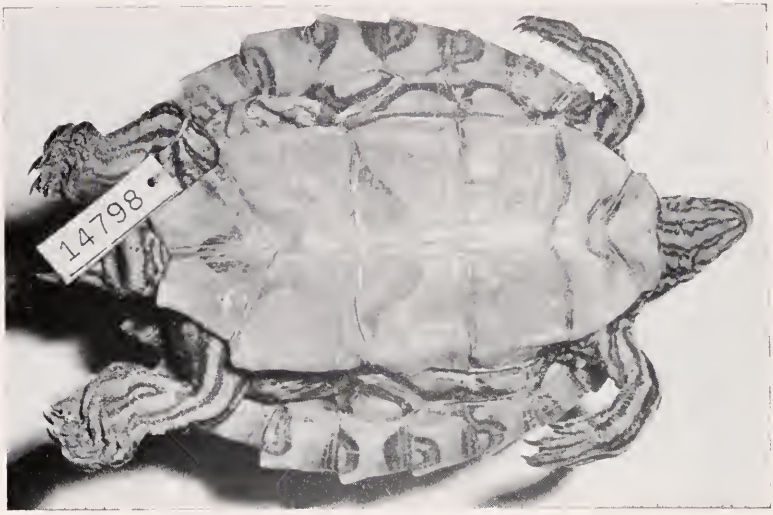


Figure 7. Ventrai view, *G. flavimaculata,* sp .nov. (Photograph by Isabelle Hunt Conant).

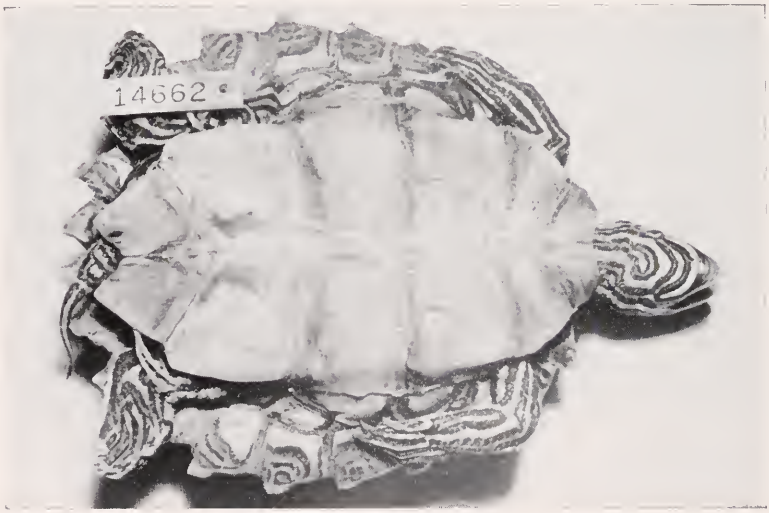


Figure 8. Ventral view, *G. nigrinoda,* sp. nov. (Photograph by Isabelle Hunt Conant).

The height is proportionately reduced in the larger turtles Pl/Ht = 1.8-2.2.

The spines of the first four vertebrals are high (height of second equals 2/3 or more lengths of seam below second and third marginal) and are much broadened and rounded. This is in sharp contrast with *flavimaculata.*

Adult males.—The adult males range from 6.80 cm to 8.00 cm in length. They have the same color pattern as the juveniles but the yellow markings of the carapace and the black markings of the plastron are more obscure. The lines of the head in the largest male (14648) are fainter and the black background is lightened.

The spines of the vertebral shields are worn and eroded in the largest specimen and do not have the broadened, rounded appearance of the spines of juveniles. The carapace edge is less serrate than in the four smaller individuals (fig. 14).

The height is reduced in the largest male in relation to plastron length (Pl/Ht = 2.0-2.2 in smaller animals; 2.3 in largest). This is primarily a reflection of the worn spines. The carapace is not narrower in the larger males, Pl/Cw = 0.9-1.0; in four smaller ones, Pl/Cw = 1.0 in largest.

The head is slightly narrower in relation to plastron length in the larger males; Pl/Hw = 5.3-5.5 in those 6.0 cm-7.1 cm in plastron length, Pl/Hw = 5.5.-6.0 in those greater than 7.5 cm in plastron length. There is a slight broadening of the alveolar surfaces in relation to head width, Hw/Aw = 5.8 in smallest, 4.8 in largest.

The third claw of the forefoot is slightly shorter than the length of the seam between the second and third marginal.

Adult females.—No adult females were collected but one was studied with binoculars and a 20 power telescope in the field. This large female retained the distinctive markings of the juveniles. The black background color of the head and the brilliant yellow markings were not reduced.

Range.—Specimens were collected from only two localities, the type locality and the Alabama River 5.5 miles east of Gosport, Monroe County, Alabama. Collecting on the Coosa River and the Mulberry Fork of the Black Warrior River did not yield this species. Its absence from these streams poses the problem of what limiting factors have prevented its movement northward. An attempt to approximate the northernmost occurrence in the Black Warrior was made June 18. A count of basking turtles was made from the juncture of Locust Fork and Mulberry Fork to the Barney Coal Mine during the period from dawn until 1 PM. No *G. nigrinoda* were observed until the river widened approximately three miles above the Barney mine. Basking turtles were common along the entire stretch. There was an apparent correlation between the occurrence of *G. nigrinoda* and the occurrence of *Amyda. Graptemys pulchra* is present in Mulberry Fork and Locust Fork.

Habitat.—Generally similar to that of *G. oculifera* and *G. flavimaculata.* All individuals were taken from brush or logs in current or

Figure 9. The distribution of *G. oculifera* (narrow vertical lines), *G. flavimaculata* (horizontal lines), and *G. nigrinoda* (wide vertical lines). The black spots indicate collecting sites; the circles indicate localities where intensive collecting has failed to produce members of this complex.

were shot from basking sites above current. Both the Black Warrior and Alabama Rivers are wider, deeper rivers than the Pascagoula or the Pearl Rivers but they also have sand and clay bottoms and moderate current in those areas where *G. nigrinoda* was collected.

This species occurs in association with *G. pulchra, Pseudemys floridana mobilensis, Pseudemys scripta elegans, Sternotherus carinatus,* and *Amyda* sp.

Bionomics.—The smallest male has a plastron length of 6.80 cm and is in the third season of growth. The largest male observed was 8.76 cm in length and had no growth zones present. No adult females were collected.

DISCUSSION

Other turtle species occurring in the Pearl, Pascagoula and the lower parts of the Tombigbee and Alabama rivers exhibit a gradual coastwise gradient in most of their characters. The populations of *Pseudemys scripta, Pseudemys floridana, Kinosternon subrubrum, Amyda ferox* and *Graptemys pulchra* of each river system are different in the percent expression of characters but much overlap is evident.

Graptemys pulchra occurs in these same stream systems as well as in the Escambia to the east and the upper reaches of the Alabama where *G. nigrinoda* is absent. However, the populations of the upper Alabama are conspicuously different from those of the lower. This

difference in parts of the Alabama is also reflected in the fact that *Graptemys geographica* occurs in the upper reaches but not in the lower.

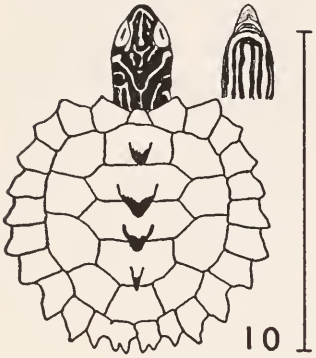
The restriction of *G. nigrinoda* to that part of the river below the fall line may be suggestive of a rather recent, rapid evolution of this complex since the exposure of the Gulf Coast in Pliocene time. There is a correlation between the northern limit of distribution and the isocryme of 15° C (as reported by Hedgpeth, 1953).

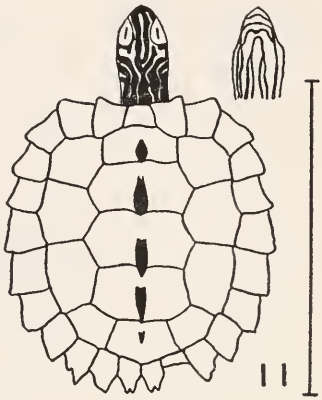
The absence of these three forms in river systems east of the Alabama and west of the Pearl is further evidence that the evolutionary history of this complex is substantially different from that of other turtle species of the Gulf Coast (fig. 9). Unfortunately there is but limited information available on the history of these river systems. The extent of the Alabama and Tombigbee systems as contrasted with the Pearl and Pascagoula is suggestive of greater age. Perhaps in this situation rests the explanation of the greater degree of divergence in *G. nigrinoda,* it perhaps being the older of the three forms. The biologist has no precise knowledge of comparative rates of evolution in the turtles but their long fossil record suggests unusually slow response. The relative youth of the Gulf Coast streams implies that rapid evolution has occurred in this complex.

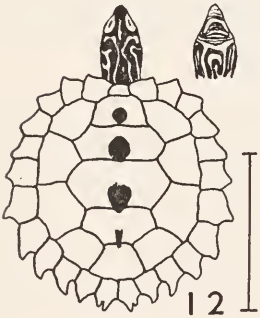
These current-dwelling turtles do not inhabit the extreme head waters and smaller tributaries as do members of the genera *Amyda, Pseudemys and Kinosternon.* There are no reports of overland movements although such observations are common for other turtles. Their isolation is thus possibly much more complete than is implied by the proximity of the drainage systems. The cohesiveness of the three groups would suggest the designation of a superspecies. This would serve to emphasize the differences between these and the remainder of the genus. Each of the three groups of populations could be designated a semispecies (Mayr, 1942; Cain, 1953).

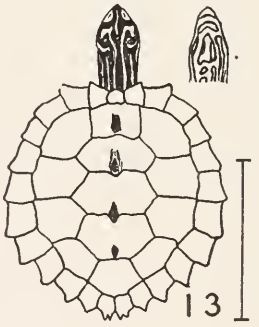
Although the three forms are basically similar in their osteology and general configuration, the morphological gap between *G. nigrinoda* and *G. flavimaculata* is much greater than that between *G. flavimaculata* and *G. oculifera* (Cagle, 1953b). Particularly striking is the contrast between the flattened carapace and knob-like projections in *G. nigrinoda* and the elevated carapace and laterally compressed spines of the other two species. An alternative taxonomic arrangement would be the recognition of *G. flavimaculata* as a subspecies of *G. oculifera* while retaining *G. nigrinoda* as a separate entity. Such an arrangement would place emphasis on the differences in degree of divergence between the forms but the evolutionary implications of such a grouping can not be justified.

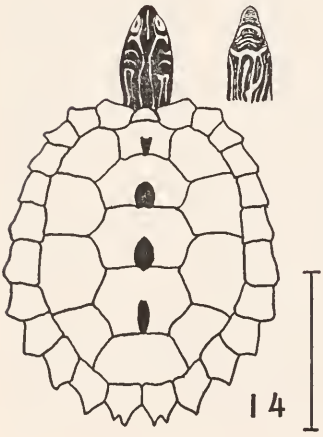
Related species of this genus do not have such striking differentiation in adjacent stream systems. *Graptemys geographica, Graptemys pseudogeographica* and *Graptemys kohni* occupy more extensive ranges without developing such gaps or steepening gradients in variation (Cagle, 1953a).

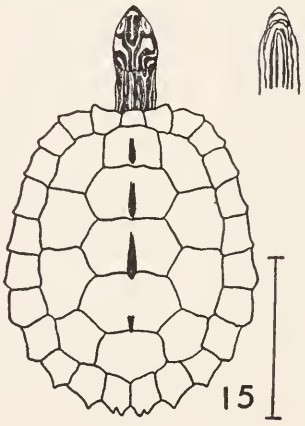

10


11


12


13


14


15

A TENTATIVE KEY TO THE GENUS *GRAPTEMYS*

This key is presented as an aid to identification of the members of this genus. It is not intended to present those characters that are of fundamental significance in establishing the patterns of speciation.

1. Length of symphysis of lower jaw ¼ longer than minimum distance between the orbits and a small triangular, yellow spot back of orbit separated from orbit by 2 to 3 diagonal yellow lines ..... *Graptemys geographica* (LeSueur)

   (Geographic turtle. Mississippi and St. Lawrence basins. Northern Louisiana north through eastern Oklahoma and Kansas to northern Minnesota; eastward through Missouri, Illinois, Kentucky, Tennessee to Vermont. Northern Mississippi, Alabama.)

   Length of symphysis of lower jaw equal to or less than minimum distance between the orbits; or, if symphysis is longer than minimum distance between orbits, no triangular spot behind eye but a large, irregular-shaped greenish or yellowish postorbital blotch present 2

2. Each costal with a large yellow-orange blotch, crescentic mark or ring. 3

   Costals without markings as described 5

3. Each costal with a large yellow or orange blotch or crescentic mark covering much of the shield. Yellow the dominant color on the ventral surface of jaw and neck ..... *Graptemys flavimaculata* n. sp.

   (Yellow-blotched sawback. Pascagoula River and tributaries, Mississippi.)

   No such markings 4

4. Each costal with one complete circle of yellow or orange formed by a line broader than the widest neck line. A yellow postorbital ovoid, rectangular or rounded spot not connected with a dorsal, longitudinal line. Vertebral spines laterally compressed ..... *Graptemys oculifera* (Baur)

Figures 10-15. Juveniles and males of *G. nigrinoda* and *G. flavimaculata;* scale line = 5 cm. **10**, Hatchling, *G. nigrinoda;* **11**, Individual in first season of growth, *G. flavimaculata;* **12**, Juvenile male, *G. nigrinoda;* **13**, Juvenile male, *G. flavimaculata;* **14**, Adult male, *G. nigrinoda;* **15**, Adult male, *G. flavimaculata.*

(Ringed sawback. Pearl River and tributaries, Louisiana and Mississippi.)

Each costal with a yellow or orange semicircle or circle formed by a line much narrower than the widest neck line. A yellow, vertical curved postorbital bar connected by a diagonal line with the postorbital bar of the opposite side. Vertebral spines knoblike ..... *Graptemys nigrinoda* n. sp.

(Black-knobbed sawback. Alabama and Black Warrior River systems.)

5. Females never developing a head as wide as ⅓ the carapace width. Postorbital mark not a large irregular shaped greenish or yellow blotch 6

Females developing a much broadened head as wide as ⅓ the carapace width. Postorbital mark an irregular bordered greenish or yellowish blotch or mark absent (see illustrations, Cagle, 1952.) 10

6. Without vertebral spines (each vertebral may be slightly elevated above next posterior one). Maximum plastron length about 16 cm. ..... *Graptemys versa* Stejneger

(Texas map turtle. Colorado River System, Texas.)

With distinct vertebral spines (absent in some individuals greater than 16 cm in plastron length.) 7

7. A postorbital vertical line extending from a dorsal longitudinal line to the base of the orbit and anteriorly under the orbit; vertical line frequently interrupted by a longitudinal line or bar ..... *Graptemys kohni* (Baur)

(Mississippi map turtle. Eastern Texas, Oklahoma, Kansas and Nebraska east to Mississippi River and southern Indiana.)

No postorbital vertical line; a comma-shaped, rectangular or ovoid postorbital mark. A series of longitudinal neck lines entering orbit below postorbital mark. 8

8. Postorbital spot, oval or elongate, much smaller than orbit, and surrounded by 2 or 3 concentric lines; 3 or 4 conspicuous longitudinal lines entering orbit; these lines alternating with thinner, less conspicuous lines. A total of 6-7 lines entering orbit; a wide yellow band extending the width of the ventral surface of the jaw; no large yellow spot beneath eye ——— *Graptemys pseudogeographica sabinensis* Cagle

(Sabine map turtle. Sabine River of western Louisiana and eastern Texas.)

Not as above. ——— 9

9. Postorbital spot not elongate but rectangular; length of rectangle extending dorso-ventrally; maximum of 5 longitudinal lines entering the eye. No wide yellow band extending the width of ventral surface of jaw but a large spot present at symphysis of lower jaw; a large yellow spot beneath eye. *Graptemys pseudogeographica ouachitensis* Cagle

(Ouachita map turtle. Louisiana northwestward into eastern Oklahoma, Kansas, Nebraska and eastward through southern Wisconsin, Illinois and southern Indiana to northern Alabama. Eastward in the Ohio River System.)

Postorbital spot comma-shaped; not rectangular; maximum of 5 longitudinal lines entering the eye; no wide yellow band extending the width of the ventral surface of the jaw; no large spot present on symphysis of lower jaw; no large yellow spot beneath the eye. *Graptemys pseudogeographica pseudogeographica* (Gray)

(False map turtle. Eastern Nebraska, southeastern South Dakota eastward through southern Minnesota and Iowa to eastern Illinois.)

10. An irregular bordered yellow bar extending completely across ventral surface of lower jaw; margins of plastral shields not bordered with black ——— *Graptemys barbouri* Carr

(Barbour's map turtle. Southwestern Georgia and Panhandle of Florida.)

No bar as described (an elongated blotch or bar may be present); margins of plastral shields bordered with black ..... *Graptemys pulchra* Baur

(Alabama map turtle. Pearl River, Louisiana eastward to Alabama, Coosa and Escambia rivers.)

REFERENCES CITED

ANDERSON, IRVING E. 1950. Surface waters of Mississippi. *Miss. State Geol. Surv., Bull.* 68: 1-338.

CAGLE, FRED R. 1952. The status of the turtles *Graptemys pulchra* Baur and *Graptemys barbouri* Carr and Marchand with notes on their natural history. *Copeia,* 1952 (4): 223-234.

_____ 1953a. Two new subspecies of *Graptemys pseudogeographica. Occ. Pap. Mus. Zool. Univ. Mich.,* No. 546: 1-17.

_____ 1953b. The status of *Graptemys oculifera. Zoologica,* 38: 137-144.

CAIN, A. J. 1953. Geography, ecology and coexistence in relation to the biological definition of the species. *Evolution,* 7(1): 76-83.

HEDGPETH, JOEL W. 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. *Publ. Inst. Marine Sci.,* 3(1): 107-224.

MAYR, E. 1942. *Systematics and the Origin of Species.* New York, Columbia Univ. Press, pp. 1-334.

LIBRARY
MAR - 3 1961
HARVARD
UNIVERSITY

TULANE STUDIES
IN ZOOLOGY

Volume 1, Number 12 August 26, 1954

THE TAXONOMIC STATUS OF THE MID-GULF COAST *AMPHIUMA*

IMOGENE R. HILL,
DEPARTMENT OF BIOLOGY, UNIVERSITY OF NEW MEXICO, ALBUQUERQUE, NEW MEXICO.

TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the area bordering the Gulf of Mexico and the Caribbean Sea. Each number is issued separately and deals with an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

EDITORIAL COMMITTEE FOR THIS NUMBER

ARNOLD B. GROBMAN, Director, Florida State Museum, Gainesville, Florida.

LAURENCE M. KLAUBER, Curator of Reptiles, Zoological Society of San Diego, San Diego, California.

ROBERT C. STEBBINS, Curator of Herpetology, Museum of Vertebrate Zoology, University of California, Berkeley, California.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected.

Separate numbers may be purchased by individuals, but subscriptions are not accepted. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers to the editor. Remittances should be made payable to Tulane University.

When citing this series authors are requested to use the following abbreviations: *Tulane Stud. Zool.*

Price for this number: $0.35.

George Henry Penn, *Editor,*
c/o Department of Zoology,
Tulane University,
New Orleans, U. S. A.

Assistants to the Editor:
Carol L. Freret
Robert E. Gordon

MUS. COMP. ZOOL
LIBRARY
MAR - 3 1961
HARVARD
UNIVERSITY

THE TAXONOMIC STATUS OF THE MID-GULF COAST *AMPHIUMA*[1]

IMOGENE R. HILL,
Department of Biology, University of New Mexico, Albuquerque, New Mexico.

The identity of the *Amphiuma* of the Gulf Coast has been studied by Ryder (1880), Cope (1886), Brimley (1909), Goin (1938) and Baker (1947). These investigators have drawn different conclusions from the study of similar material. Their conclusions have been based on analyses utilizing either one or several of the following characters: number of toes, color, ratio of total length to body length, number of costal grooves and ratio of body length to limb lengths.

The early investigators, Ryder, Cope and Brimley, had only a small number of individuals available for their studies. The more recent workers, Goin and Baker, considered populations of individuals, but none of the investigators, measured or dealt with ontogenetic variation, allometric growth or sexual dimorphism. Since some authors give only the mean of the ratios and of the costal groove number, it is not possible to evaluate the characters reported. A new approach was required to evaluate the characters previously used and to investigate other differences, if any, between the populations.

Historical—Garden described *Amphiuma means* in 1821. In 1827 Cuvier described a three-toed individual as *Amphiuma tridactylum* and compared it with a two-toed one: "This description of the *Amphiuma* of three digits agrees nearly in everything to the kind with two digits. Its general form is the same; its diameter is one-twentieth of its length; the length of its head is nearly one-fourteenth; its tail is exactly one-fourth. It has similar folds on each side. Its color is the same. Summarizing, it is necessary for descriptive purposes to look closely at its extremities. Then one sees that each of its limbs is divided into three perfectly distinct toes; it is in reality its only exterior character which is readily discernable."

The three-toed individuals were placed in the genus *Mauraenopsis* by Fitzinger (1843). Ryder (1880) studied a series of young *Amphiuma* from Biloxi, Mississippi and reestablished the three-toed salamander in the genus *Amphiuma.* Ryder based his classification solely on the number of digits. He stated "so that in some the number of digits (two) is characteristic of *Amphiuma,* and in others (three) they are characteristic of *Mauraenopsis.*" Cope (1886) could not separate his specimens into two-toed and three-toed groups and so he classified all individuals, regardless of the number of toes, as *Amphiuma means.*

Brimley (1909) called the three-toed animal *Amphiuma tridactylum.* Brimley stated that the three-toed specimens differed from the

[1] From a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science of the Graduate School of Tulane University.

two-toed ones in being lighter in color on both the dorsal and ventral surfaces and in being distinctly bicolored; the limbs of the three-toed *Amphiuma* were "more strongly developed." The character used in separating the two forms, prior to 1909, was number of toes. Brimley also reported that he had never seen a two-toed individual which had attained as great a size as the three-toed ones; one three-toed individual examined by Brimley was 736.6 mm in length.

Goin (1938) examined 206 individuals and found that the costal groove count and the ratio of total length to body length may also be used as taxonomic characters. Considering the region where the two ranges meet, he stated "coloration, costal groove count and ratio of total length to body length change more or less gradually, but the two-toed specimens of the east interdigitate with the three-toed specimens of the Mississippi Valley." According to Goin, *Amphiuma means means* is a two-toed, unicolored animal with 57-60 costal grooves and a ratio of total length to body length which averages 1.33. *Amphiuma means tridactylum* is a three-toed, bicolored animal with 60-64 costal grooves and a ratio of total length to body length which averages 1.29. Goin considered the area of intergradation as the region between Lake Pontchartrain in southeastern Louisiana and Liberty County, Florida.

Baker (1947) examined over 280 *Amphiuma* and concluded that "two species of Amphiumae, *Amphiuma means* and *Amphiuma tridactylum,* occur, each occupying a distinct ecological range." Baker found no evidence of intergrades and stated that all known specimens could be designated as one of these species by the "valid species characters of number of toes, body length in total length, length of limbs in body length and coloration."

Procedures

Number of toes and coloration—In the course of this investigation, 537 *Amphiuma* were examined. Two hundred and forty-six of these were two-toed, two hundred and eighty-eight were three-toed, and three individuals had both two- and three-toed limbs (Table 1). All individuals examined are placed into one of six arbitrary geographical series to determine the degree of difference, if any, between the series. Series 1 includes all three-toed *Amphiuma* from the west bank of the Mississippi River westward. The most western locality of an *Amphiuma* examined in this study is nine miles northwest of Saratoga, Hardin County, Texas. Series 2 consists of the individuals from Audubon Park in New Orleans, Louisiana. Series 3 includes all individuals in the alluvial valley east of the Mississippi River. Included in Series 4 are the three-toed *Amphiuma* from the region east of the alluvial valley of the Mississippi River to western Alabama. This series includes individuals from extreme southeastern Louisiana and Mississippi.

Series 5 consists of the two-toed individuals from the same geographical area as Series 4, and Series 6 consists of those individuals from the Atlantic coastal states westward to Liberty County, Florida

TABLE 1.
NUMBER OF TOES

Series	Number with Two Toes	Number with Uncertain Number of Toes	Number with Three Toes	Total Number Examined
1	0	0	33	33
2	0	0	191	191
3	0	0	17	17
4	0	3	47	133
5	83		0	
6	163	0	0	163
Total	246	3	288	537

Figure 1. Distribution of the 537 *Amphiuma* examined in this research. The circular and X-shaped symbols represent three-toed and two-toed individuals respectively.

(figure 1). The individuals from western Alabama to Liberty County, Florida, were not placed into any of the six series because they were too few in number to constitute an additional series. Series 4 and 5 extend as far east as the locality where both the two-toed and the three-toed individuals are found in close association. This arbitrary grouping into series does not mean to imply that the individuals from western Alabama to Liberty County, Florida, are different from those in Series 4 and 5.

Most of the specimens utilized in this study are deposited in the collections of Tulane University (TU); a few were borrowed from the American Museum of Natural History, the United States National Museum, and the University of Florida.

An external morphological study was made on each individual. The following information was recorded: museum catalogue number, date collected, collector, tail length, body length, hind-limb length, fore-limb length, head length, number of toes, sex and coloration. The length of the tail was taken as the distance from the anterior end of the cloacal opening to the tip of the tail. The limbs were pressed posteriorly and horizontally along the body and the lengths were recorded as the distances from the base of the limb to the distal end of the longest digit. In the three-toed individuals, the longest digit is the middle one and the outermost toe is the smallest (when the limbs are pressed posteriorly and horizontally along the body). The measurements were made consistently on the right limbs of the animals unless the right limbs were mutilated. The head length was taken as the straight line distance from the anterior end of the brachial fissure to the tip of the nose. The number of toes on each limb was recorded in a formula arrangement, *e.g.* 2/2 2/2.

The formula is read from left to right, and the numbers represent, respectively, the number of toes on the right fore-limb, the number of toes on the left fore-limb, the number of toes on the right hind-limb and the number of toes on the left hind-limb. If the individuals were sexed, this was done by dissection. The dorsal, ventral and throat colorations were recorded. Table 2 indicates the throat coloration of the specimens from the six geographical series.

The measurements were made with vernier calipers, except when the structure was greater than 125 mm. In the latter case or if the preserved animal were coiled, a string was used and transferred to a ruler calibrated in millimeters. The measurements were recorded to the nearest millimeter. All of the measurements were made on preserved specimens. There is undoubtedly some differential shrinkage between the various body parts, resulting from the preservation, but this possible error is likely to be minimized since all of the individuals examined were preserved by comparable methods.

Only those individuals were measured whose parts were not mutilated. Mutilation could usually be detected by the presence of scar tissue. Frequently, *Amphiuma* have part of a limb or an entire limb missing. Obviously, it is easier to detect a mutilation which has

TABLE 2.
THROAT COLORATION

Series	Number without Throat Patch	Number with Uncertain Throat Color	Number with Throat Patch	Total Number Examined
1	0	0	33	33
2	0	0	191	191
3	0	0	17	17
4	0	3	47	133
5	83		0	
6	163	0	0	163
Total	246	3	288	537

occurred recently in the life of an animal than it is to determine one which occurred very early in the life of the individual. It is unusual to find all four limbs of an animal mutilated. The hind-limbs are normally longer than the fore-limbs, except in individuals less than a hundred millimeters in length. One can usually confirm the opinion of whether or not a digital mutilation has occurred by comparing the measurements of all four limbs.

Body proportions—Heretofore, three assumptions have been made by some workers who have considered body proportions as taxonomic characters in *Amphiuma.* These assumptions include absence of sexual dimorphism, high correlation between the dimensions of the body parts, no ontogenetic variation. The latter is illustrated by Baker's use of simple ratios, implying that body proportions do not change with an increase in age (body length).

If these assumptions represent the facts, then the previous work is valid, but if one or more of the assumptions are incorrect, the results may require some qualification. Statistical methods can often be used to give quantitative estimates of these assumptions. The preliminary procedure was to determine the presence or absence of sexual dimorphism, the degree of correlation between the body parts, and whether or not ontogenetic variation was present.

To determine the presence or absence of sexual dimorphism, four groups of graphs were set up, each group being composed of six graphs representing the six geographical series. The four groups represent the following four body proportions: head length to body length, fore-limb length to body length, hind-limb length to body length and tail length to body length. For each graph the horizontal scale represents the body length in millimeters and the vertical scale represents the other body part. The presence or absence of important sexual dimorphism can be estimated by inspection. An inspection of the scattergrams indicates that the males and females do not fall

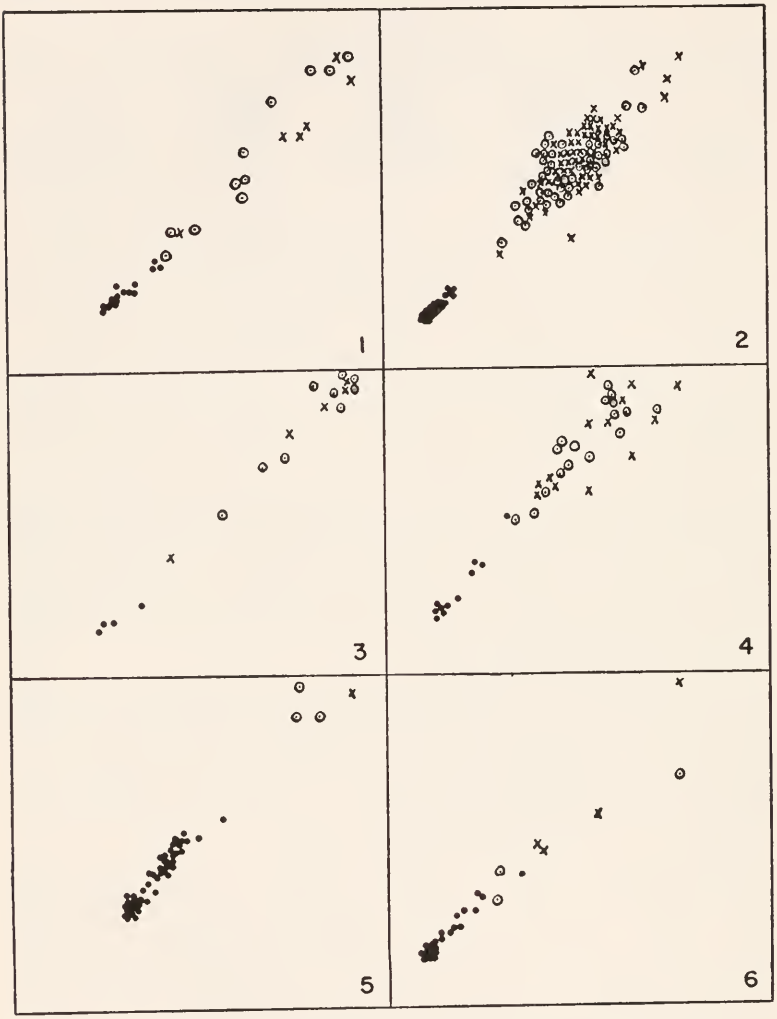


Figure 2. Scattergrams showing the relationship of head length to body length for each of the six series. The three symbols, X, circle with dot and plain dot, identify respectively male, female and unsexed individuals.

into two separate groups in any of the series; therefore, if sexual dimorphism exists it is negligible (figures 2-5).

Obviously, there is a definite relationship of head length, fore-limb length, hind-limb length and tail length to body length so the problem is concerned with the degree of correlation and the nature of the correlation (*e.g.,* simple and linear). The degree of correlation of

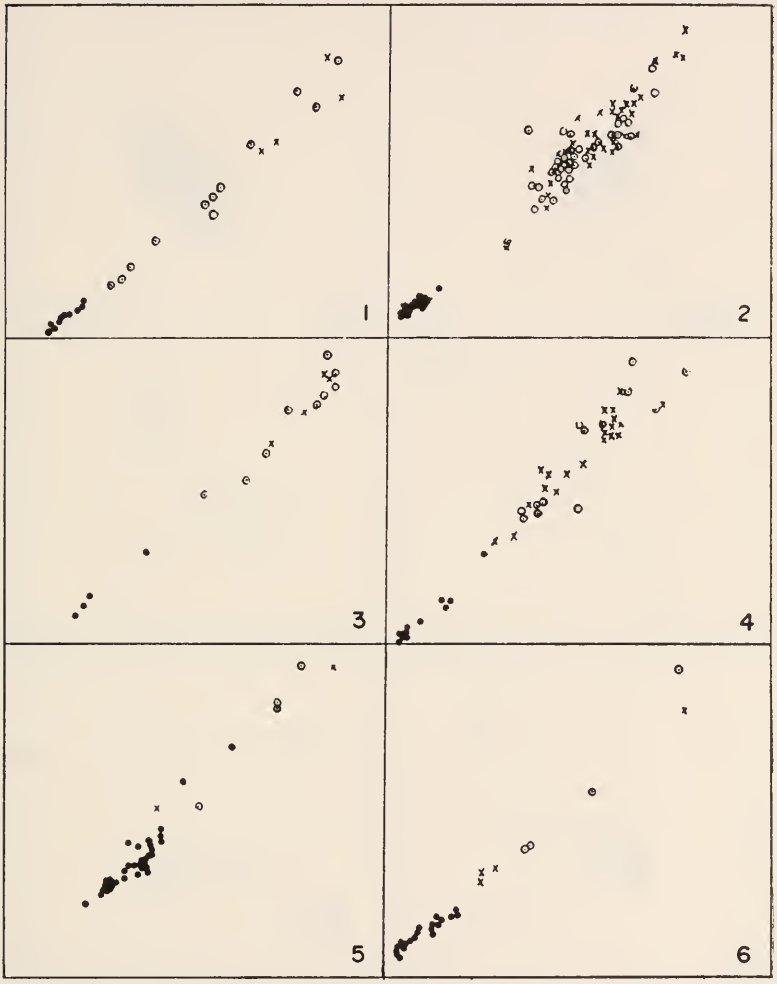


Figure 3. Scattergrams showing the relationship of fore-limb length to body length for each of the six series. Symbols as in fig. 2.

the various body parts with the body length was determined by calculating the correlation coefficients (Tables 3-6). The method used was Pearson's product-moment method using grouped data cross-tabulated. Twenty-four correlation tables were constructed. In constructing the correlation tables, the body length was considered the independent variable and the other body part length the dependent variable (Peatman, 1947).

Ontogenetic variation—To determine whether or not body pro-

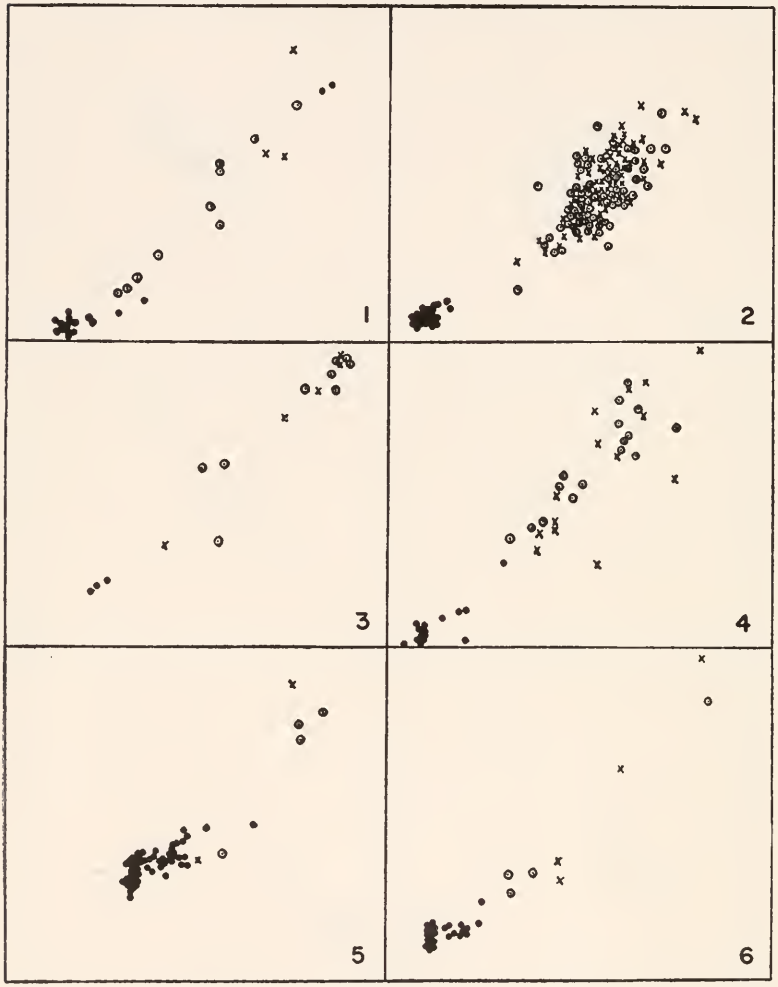


Figure 4. Scattergrams showing the relationship of hind-limb length to bo dylength for each of the six series. Symbols as in fig. 2.

portions remain constant as the animal increases in age (length), the regression lines for the four body parts of each of the six series were calculated. The correlations in ontogenetic series are nearly always high, but inspection of the scattergrams indicate that linearity may be assumed for practical purposes.

The fact that the line is linear for the four body proportions of each of the six series was established by the product-moment correlation coefficients. Thus, the regression equation for the straight line is:

$$X = a + aB$$

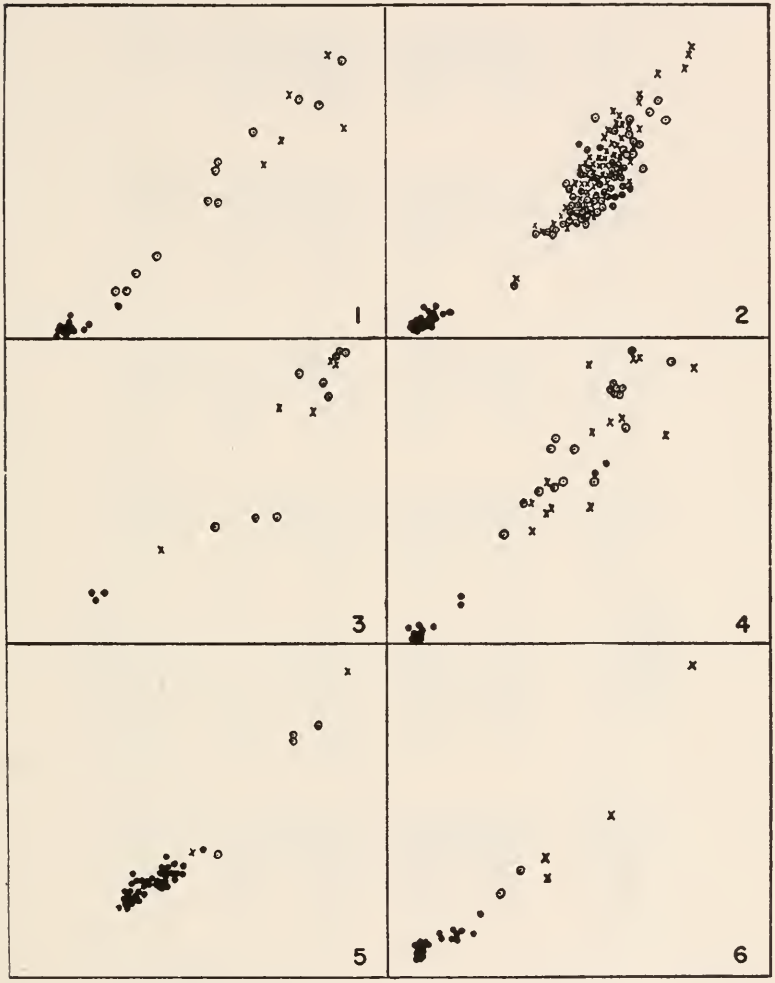


Figure 5. Scattergrams showing the relationship of tail length to body length for each of the six series. Symbols as in fig. 2.

where X is equal to either head length, fore-limb length, hind-limb length or tail length; a and b are the regression constants and B is the body length corresponding to a particular X length. In order to determine X for any particular body length, B, the regression constants must be calculated.

The three methods suggested by Klauber (1943) for calculating the regression constants are: (1) analytical methods, (2) method of least squares and (3) the graphical method. Of these, the latter was

TABLE 3.
RELATIONSHIP OF HEAD LENGTH TO BODY LENGTH

Series	1	2	3	4	5	6
Total number of individuals	33	191	17	47	84	163
Body length range, mm	63.5-566.8	43.2-535	51.5-504.5	73.1-563.3	63-442.1	45.1-600
Correlation coefficient, r	0.981	0.936	0.985	0.968	0.919	0.989
	± 0.0044	± 0.0061	± 0.020	± 0.0063	± 0.011	± 0.0012
Regression constants	**a** 0.82	**a** 1.034	**a** 0.262	**a** 0.605	**a** 1.650	**a** 1.830
	b 0.125	**b** 0.119	**b** 0.116	**b** 0.109	**b** 0.096	**b** 0.090
Restricted number of specimens	13	68	12	21	5	8
Body length range, mm	330.6-566.8	350.8-535	341.6-504.1	353.3-563.3	285-442.1	249.1-600
Standard body length, mm	400	400	400	400	400	400
Standardized head length range, mm	39.3-59.7	35.6-51.2	40.5-51.4	34.3-52.8	40.1-45.8	38.5-49.5
Mean head length equated to standard body length, mm	47.54	43.1	44.8	45.02	44.0	41.3
Standard error of mean, mm	± 1.38	± 0.233	± 0.92	± 0.86	± 0.95	± 1.40
Standard deviation, mm	4.97	4.00	3.05	3.86	1.90	3.71

TABLE 4.
RELATIONSHIP OF FORE-LIMB LENGTH TO BODY LENGTH

Series	1	2	3	4	5	6
Total number of individuals	33	191	17	47	84	163
Body length range, mm	63.5-566.8	43.2-535	51.5-504.5	73.1-563.3	63-442.1	45.1-600
Correlation coefficient, r	0.962	0.919	0.595	0.929	0.901	0.968
	± 0.089	± 0.0074	± 0.104	± 0.013	± 0.017	± 0.0034
Regression constants	a 1.404	a 1.68	a 1.72	a 0.329	a 0.526	a 1.34
	b 0.0234	b 0.0297	b 0.0261	b 0.0276	b 0.021	b 0.0207
Restricted number of specimens	13	68	12	21	5	8
Body length range, mm	330.6-566.8	350.8-535	341.6-504.1	353.3-563.3	285-422.1	249.1-600
Standard body length, mm	400	400	400	400	400	400
Standardized limb length range, mm	9.3-14.2	9.1-13.5	10.1-13.0	7.0-13.2	6.2-8.9	6.8-10.9
Mean fore limb length equated to standard body length, mm	10.90	10.90	12.09	11.25	7.99	8.50
Standard error of mean, mm	± 0.257	± 0.164	± 0.250	± 0.427	± 0.121	± 0.576
Standard deviation, mm	0.894	1.35	0.83	1.86	0.767	1.41

TABLE 5.
RELATIONSHIP OF HIND-LIMB LENGTH TO BODY LENGTH

Series	1	2	3	4	5	6
Total number of individuals	33	191	17	47	84	163
Body length range, mm	63.5-566.8	43.2-535	51.5-504.5	73.1-563.3	63-442.1	45.1-600
Correlation coefficient, r	0.979	0.943	0.926	0.952	0.909	0.949
	± 0.0049	± 0.0055	± 0.036	± 0.0093	± 0.013	± 0.0078
Regression constants	a 0.18	a 1.033	a 0.72	a 1.224	a 0.0351	a 1.572
	b 0.0422	b 0.0417	b 0.0431	b 0.0368	b 0.0319	b 0.0237
Restricted number of specimens	13	68	12	21	5	8
Body length range, mm	330.6-566.8	350.8-535	341.6-504.1	353.3-563.3	285-442.1	249.1-600
Standard body length, mm	400	400	400	400	400	400
Standardized limb length, range, mm	15.2-18.9	13.1-20.1	14.7-18.8	11.8-23.8	9.8-14.2	9.5-14.0
Mean hind limb length equated to standard body length, mm	17.27	16.49	18.38	17.35	12.75	11.70
Standard error of mean, mm	± 0.148	± 0.034	± 0.139	± 0.445	± 0.316	± 0.596
Standard deviation, mm	1.33	1.53	1.24	2.91	1.26	1.73

TABLE 6.
RELATION OF TAIL LENGTH TO BODY LENGTH

Series	1	2	3	4	5	6
Total number of specimens ..	33	191	17	47	84	163
Body length range, mm	63.5-566.8	43.2-535	51.5-504.1	73.1-563.3	63-442.1	45.1-588.3
Correlation coefficient, r	0.924	0.998	0.981	0.931	0.960	0.860
	± 0.017	± 0.00020	± 0.0062	± 0.013	± 0.0057	± 0.014
Regression constants	a 2.976	a 4.005	a 3.173	a 4.209	a 2.775	a 5.53
	b 0.338	b 0.343	b 0.353	b 0.362	b 0.380	b 0.389
Restricted number of specimens	13	68	12	21	5	8
Body length range, mm	330.6-566.8	350.8-535	341.6-504.1	353.3-563.3	285-442.1	294.3-588.3
Standard body length, mm ..	400	400	400	400	400	400
Standardized tail length range, mm	112.8-166.6	99.8-149.8	127.9-160.0	105.5-187.4	132.4-169.0	129.7-170.2
Mean tail length equated to standard body length, mm	138.5	127.05	140.2	137.2	145.9	148.95
Standard error of mean, mm	± 4.42	± 1.48	± 2.32	± 4.20	± 4.10	± 5.78
Standard deviation, mm	15.30	12.17	7.70	18.70	8.20	14.16

chosen, the reason being that the same graphs used to determine sexual dimorphism could be used to determine the regression constants.

After obtaininng *a* and *b* for each of the four body proportions for each of the six series, these constants were substituted in their respective regression equations.

From a study of the regression lines, it was determined that the body proportions do not remain constant throughout life. The reason for the foregoing statement is that *a* is not equal to zero (the regression line does not pass through the origin) (Klauber, 1943). However, it should be mentioned that in some cases *a* is almost equal to zero; although, additional collections may or may not reduce *a* to zero. If the proportion remains constant throughout life, the relationship of the head length to the body length should be the same in the adults as it is in the juveniles. If a juvenile with a body length of 50 mm is substituted in the regression equation ($H = 1.034 + 0.119B$), the value of *H* is equal to 6.984 mm. If an adult body length of 600 mm is substituted in the regression equation, *H* is equal to 72.434 mm. The juvenile head length is 14 percent of its body length; the adult head length is only 12 percent of its body length. This indicates that the juveniles have proportionately larger heads than the adults; therefore, the proportionality does not remain constant with an increase in body length.

Standardization—Since there were insufficient numbers of individuals of a single body length in each series, a second method suggested by Klauber was utilized to eliminate ontogenetic variation. This method requires the conversion of the head length, fore-limb length, hind-limb length, and tail length of the individual to a standard body length. In using this method, the assumption was made that any specimen in growing to (or returning to) the standard body length does so by maintaining a constant percentage deviation from the regression line (Klauber, 1941). The standard body length was arbitrarily chosen as 400 mm. In determining the standard body size, the writer was guided by the known biology of *Amphiuma* so that the chosen body length would be within the adult (sexually mature) body length range of the individuals of each of the six series. The females of the Audubon Park population become sexually mature when they attain a body length of 330 mm but the individuals of the Audubon Park population do not attain a size as large as that of *Amphiuma* collected from the surrounding areas (Cagle, 1948). The 400 mm body length should include the sexually mature individuals from all geographical series.

The body length range for the restricted number of specimens was chosen to include the greatest number of individuals, the limiting factor being the exclusion of individiuals less than 249 mm in body length or greater than 600 mm in body length (Tables 3-6). The statistical accuracy sacrificed by limiting the study to fewer specimens (by taking a narrow range) is more than compensated for by the elimination of possible errors in translating the specimens

over too great a distance along their regression lines (Klauber, 1938).

The actual measurements of the body parts of each individual within the restricted ranges were converted to the measurement they would probably have at 400 mm body length by substituting the actual measurements in a standardization formula (Klauber, 1941).

A survey of the available material indicated that a moderate number of individuals (all sizes included) were available in Series 1 through 4, but the number in the restricted size range of Series 5 and 6 was very small. The range could not be widened because the millimeter spread on either side of the mid-point could not exceed 200 mm (Klauber, 1938). Klauber has used as few as five individuals in his snake studies.

In order to determine the standardized body parts for each individual of each series, the individuals from the restricted ranges of Series 1 through 6 were standardized by substituting the actual length of the part and the body length in a standardization formula. The estimated head length that the *Amphiuma* would have at the standard body length of 400 mm is 34.33 mm. Standardized lengths of the body parts, computed for the restricted number of specimens, were gathered into an array (separate for each geographical series) and their statistics computed (Tables 3-6).

Graphical relationships—Bar graphs were constructed to show the relationship of the range, standardized mean, standard error of the mean and the standard deviation of the four body parts for each of the six series. The horizontal axis was calibrated to include the range of the standardized measurements. For each series (geographical locality) the range of variation is shown by a horizontal line and the mean (M) by a short vertical line. The blackened part of each bar comprises two standard errors of the mean ($2\sigma_M$) on either side of M. One-half of each black bar plus the white bar at either end outline one standard deviation (σ) on either side of M. Standard deviation indicates dispersion and two standard errors of the mean indicates reliability (Hubbs and Hubbs, 1953).

Results

Number of toes and coloration—The division of the 537 individuals into the six geographical series shows the Audubon Park individuals (Series 2) to be the most numerically representative of any of the series. Series 6, 5, 4, 1, and 3 follow, respectively, in decreasing numbers. The division of the individuals into size groups of 50 mm to determine the adequacy of the various age groups of each series, yielded the following information: of the three-toed groups, Series 1 was not represented in the size groups of less than 50 mm, of 250-300 mm, and of 350-400 mm; Series 2 was not represented in the size groups of 100-150 mm and 550-600 mm; Series 3 was not represented in the size groups of less than 50 mm, 100-150 mm, 200-250 mm, and 550-600 mm; Series 4 was not represented in the size group of less than 50 mm. The groups not represented

in the two-toed populations by Series 5 are size groups of less than 50 mm, 300-350 mm, 450-500 mm, 500-550 mm, 550-600 mm; by Series 6, 300-350 mm, 450-500 mm, and 500-550 mm (figures 6 and 7).

An inspection of the map showing the geographical distribution of the individuals examined in this research indicates that the two-toed and three-toed individuals occur together in the region where the alluvial valley of the Mississippi River meets the East Gulf Coastal Plain (figure 1). Within this region the proximity of the three-toed *Amphiuma* to the two-toed *Amphiuma* varies. A collection made in Amite, Louisiana, June 8, 1948, consisted of 42 *Amphiuma* taken from the same mud hole; of these, forty-one individuals had two toes on all four limbs and one individual had three toes on all four limbs. There is reason to believe that these individuals are from the same brood. All except one individual had a body length of approximately 214 mm. In the same region individuals with two toes on all four limbs and individuals with three toes on all four limbs have been collected together, either in the same drainage ditches, in adjacent drainage ditches or within a few miles (less

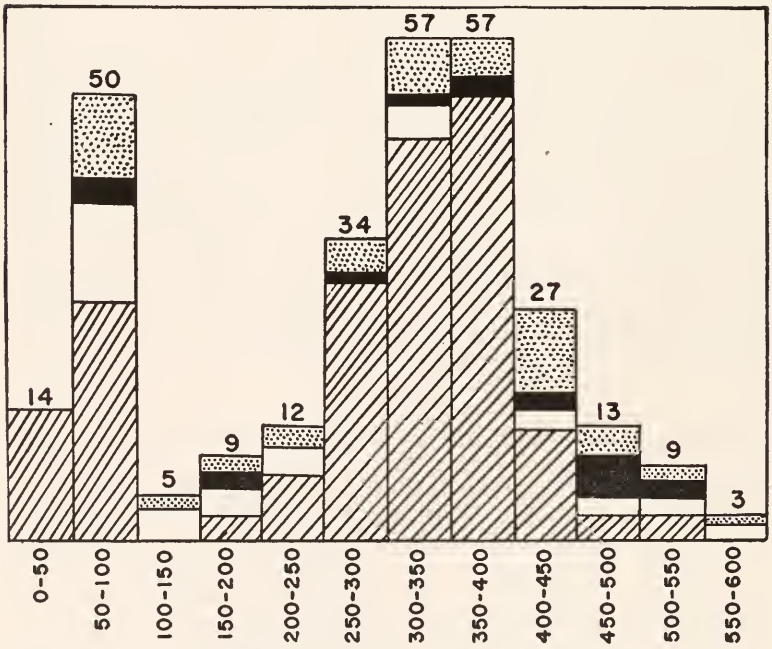


Figure 6. The distribution of body lengths of 290 specimens: Audubon Park (cross-hatched), west of the Mississippi River (clear), eastern alluvial valley (shaded), and Series 4 (stippled). The total number of individuals composing each 50 mm size group is given at the top of each bar of the histogram.

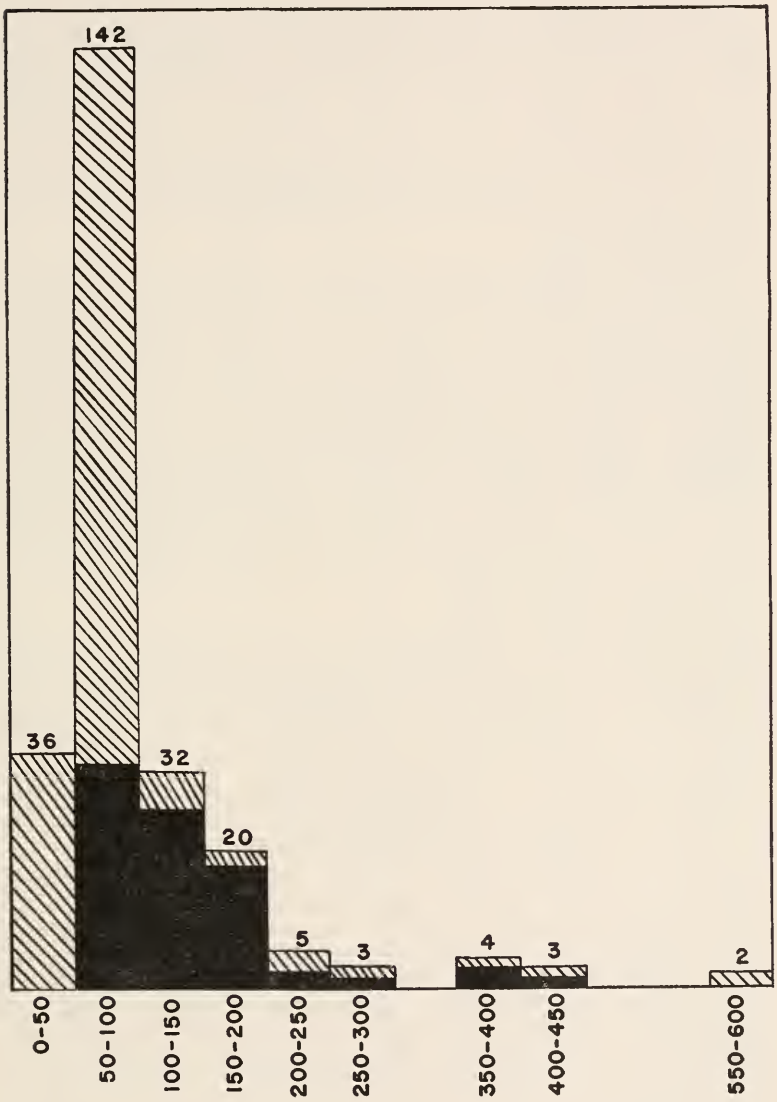


Figure 7. The distribution of body lengths of 83 specimens from Series 5 (shaded) and 163 specimens from the Atlantic coastal states (cross-hatched). The number of individuals comprising each 50 mm size group is given at the top of each bar of the histogram.

than five) of each other.

Three individuals with both two-toed and three-toed limbs on the same individual have been collected within this same geographical area. One of these was collected in Mandeville, Louisiana, in August, 1924, and the other two individuals were collected three miles north of the town of Pearl River, Louisiana. Both of these individuals were collected within the critical area (Series 4 and 5). The one from Mandeville (TU 2207) has a body length of 235.5 mm. The ones collected north of Pearl River in January, 1949 (TU 4777), and January, 1950 (TU 11414), have body lengths of 356 mm and 433 mm respectively.

Courtship activity between a two-toed and a three-toed *Amphiuma* has never been reported. The males of the Audubon Park series are reproductively active from mid-January to mid-May (Cagle, 1948). It is possible that in the region where the alluvial valley of the Mississippi River meets the East Gulf Coastal Plain, the two-toed and three-toed *Amphiuma* are reproductively active at the same time. The reason for the foregoing statement is that a two-toed male *Amphiuma* collected one mile north of Covington, Louisiana, March 6, 1950, was in a reproductive condition. The cloaca of this male was red, swollen and partially everted. The animal had more than ten well defined teeth prints and cuts on its body. These teeth marks and cuts may indicate fighting between the males during the reproductive season (Cagle, 1948).

All individuals examined could be placed into one of the two groups on the basis of number of toes except the three peculiar individuals, or 0.56 percent of the population. The toe formula for the individual from Mandeville is 2/2 3/3; for the two Pearl River specimens, the formulae are 2/2 3/2 and 3/2 2/3. All individuals of the six geographical series can be definitely separated into two-toed groups and three-toed groups on the basis of color, with the exception of the same three individuals which cannot be separated into one of two groups on the basis of the number of toes.

Within the three-toed group there are various degrees of ventral pigmentation, but the overall coloration is never so dark as that of the two-toed individuals. Whether this variation in the ventral coloration within the three-toed group is due to the effects of preservation, ecology, or inheritance has not been determined. The percentage of individuals of two of the three-toed series with ventral pigmentation is as follows: 7.8 percent for the Audubon Park individuals and 19.1 percent for those examined in Series 4. The individuals from the eastern alluvial valley usually have a mottled ventral surface.

Characteristically, the three-toed individuals have a black throat patch. The two-toed individual has no throat patch. Two of the three individuals, which cannot be separated into either the two-toed or the three-toed groups on the basis of a consistant number of toes and coloration, do not have a characteristic black throat patch, but

one of the individuals does have an indication of a throat patch.

Body proportions—Although the ontogenetic spread is comparatively satisfactory for the six series, the frequencies of all size groups should be increased, with the possible exceptions of the eastern two-toed juveniles (50-100 mm) and the Audubon Park adults (300-400 mm).

The correlation coefficients (r) are all high except that for forelimb length to body length of Series 3 (0.595). No explanation is attempted for this low correlation coefficient.

The values for standard deviation (σ) are calculated on the assumption of normal distribution which is not likely to be realized in small samples. There are reasons for distrusting the reliability of the difference that is indicated by the graphical method when the samples include fewer than thirty specimens. Consequently, the limitation of the graphs (figures 8-11) is realized. The graphical analysis indicates why a broad overlap of the dark bars indicates low reliability of the observed difference between two samples and why any considerable separation of these bars indictates a high reliability. The plotting of one standard deviation on either side of the mean indicates an 84 percent separation.

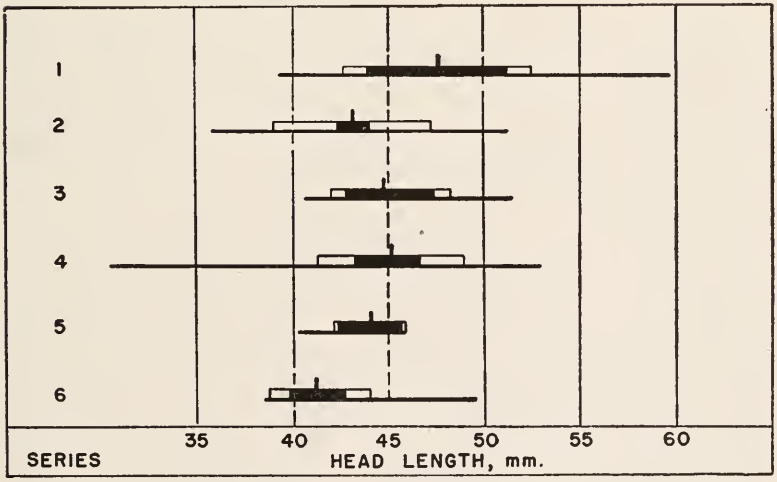


Figure 8. Bar graphs showing the relationship of the range, mean, standard deviation and standard error of the mean for head length for each of the six series. For each locality the range of variation is shown by a horizontal line; the mean (M), by a short vertical line. The blackened part of each bar comprises 2 standard errors of the mean (2 σ M) on either side of M. One-half of each bar plus the white bar at either end outline 1 standard deviation (σ) on either side of M.

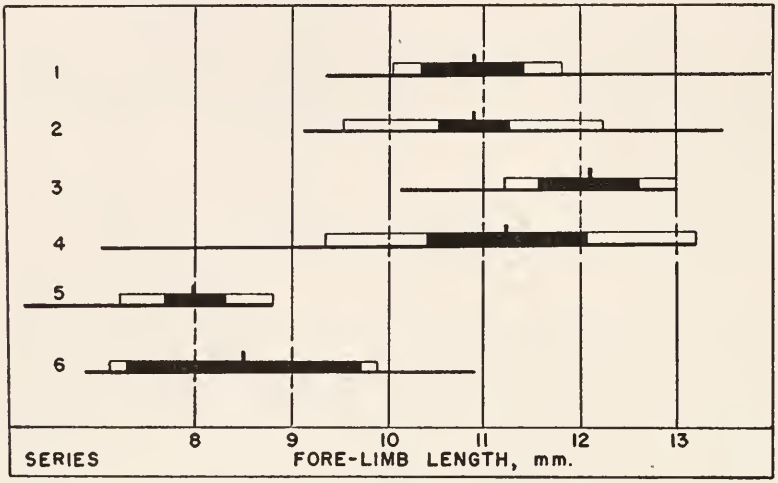


Figure 9. Bar graphs showing the relationship of the range, mean, standard deviation and standard error of the mean for fore-limb length. Arrangement as in fig. 8.

Discussions and Conclusions

Number of toes and coloration—The separation of *Amphiuma* into three groups on the basis of number of toes and coloration gives rise to the question as to whether or not the smallest of the three groups, comprising 0.56 percent of the population, is an intergrade group. If the coloration of these three individuals is due to either ecology or to methods of preserving the animals, and if the variation in the number of toes is due to either mutilation or to the inheritance of the monodactyly or polydactyly type, then *Amphiuma* can be completely separated into two groups, indicating no intergradation.

Since other individuals occurring within the same ecological area do not have the same coloration as these three individuals, indicates that ecology *per se* is not the causative factor in producing this coloration, unless the ecological factor producing it is extremely localized. The latter assumption is unlikely; for, if *Amphiuma* is so susceptible to these extremely localized conditions, a greater degree of natural variation would be expected among the remaining individuals than has been found. It is interesting that the type of coloration shown by these three individuals, which may be a blending resulting from the interbreeding of a bicolored individual with a unicolored individual, is found only in the region where the ranges of the two-toed and the three-toed individuals meet and overlap.

The fact that these three animals have no apparent scar tissue and that the measurements of the left limbs are the same as those of their corresponding right limbs constitutes evidence against the occurrence of mutilation. It is true that monodactyly and polydactyly

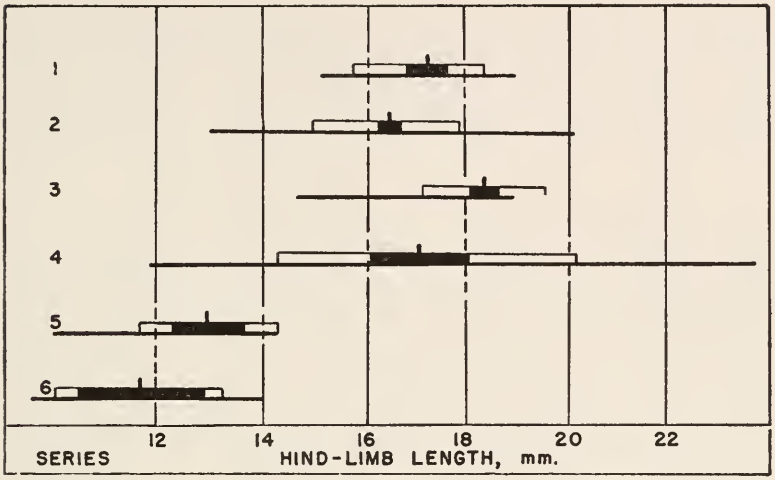


Figure 10. Bar graphs showing the relationship of the range, mean, standard deviation and standard error of the mean for hind-limb length. Arrangement as in fig. 8.

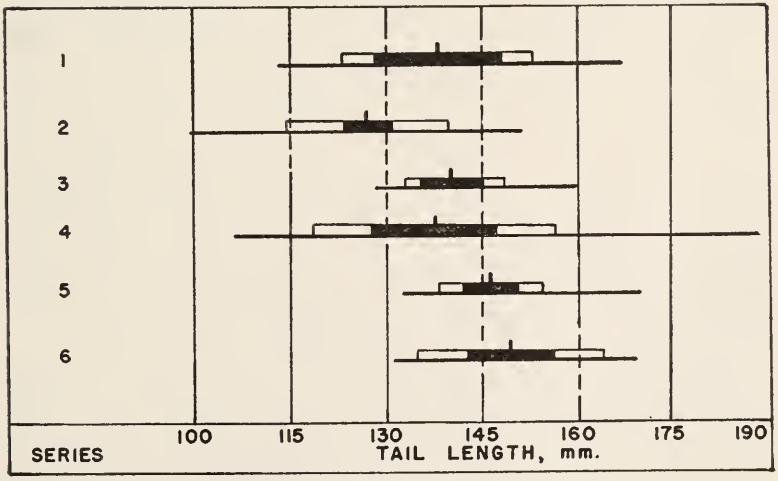


Figure 11. Bar graphs showing the relationship of the range, mean, standard deviation and standard error of the mean for tail length. Arrangement as in fig. 8.

occur in *Amphiuma,* but it is not evident that either one of these conditions expresses itself in any of the three individuals. Polydactyly has been observed only in individuals in the three-toed series, which series were designated by number of toes, coloration (general body color and the presence of throat patch), and geographical location. TU 4777 would have to be considered a three-toed individual because of the presence of the throat patch. The toe formula 2/2 2/3 must then be a result of inheritance (didactyly) as there is no evidence of mutilation. TU 2207 and TU 11414 because of the absence of a throat patch would be considered two-toed individuals. The toe formulae, 2/2 3/3 and 3/2 2/3, respectively, for TU 2207 and TU 11414 must be explained also by inheritance (polydactyly); however, polydactyly has not been observed in two-toed individuals (concerning geographical ranges) in this collection. In spite of the assumption of the presence of polydactyly, and the fact that the throat patch separates the three individuals into two groups, the uniform coloration of the three individuals and the almost identical general coloration of two of the individuals, TU 4777 with the throat patch and TU 11414 without the throat patch, prevents these three individuals from being separated into one of two groups.

Basically, the taxonomic position of the Mid-Gulf Coast *Amphiuma* resolves itself into the taxonomic position of these three individuals; that is, whether or not the three can be separated into one of two groups, a two-toed or a three-toed group, or whether all three should be placed into a third group, an intergrade group. The question is whether these three intermediates are true subspecies or hybrids.

With the exception of three specimens, all two-toed specimens have one toe pattern and all three-toed specimens have another. Since the two tables (1 and 2) are generally concordant and the forms (consistent with respect to two different characters, number of toes and pattern) are also sympatric in southeastern Louisiana (at least), and, in some cases, in the same pond, we are probably dealing with two separate species. It is difficult to conceive of two characters as different as number of toes and pattern that would result from a single genic element. If we were dealing with true subspecies and an area of intergradation, we should expect to find an almost complete mixture of characters in the intergrading area; that is, two-toed individuals with all variations in pattern and three-toed individuals with the same diversity. Intergradation is indicated in only three specimens out of 131 from the critical area (Series 4 and 5).

On the basis of this investigation the writer considers the three individuals to be hybrids. If there were a high proportion of mixed individuals in the critical area, the case for intergradation and a subspecific relationship would be greatly strengthened, particularly if the characters typifying the two groups were well jumbled in the intermediates. More individuals need to be collected from the critical area (Series 4 and 5).

Body proportions—The indication of species separation is further

reinforced by the fact that three-toed individuals, as a group, differ from the two-toed in proportionate limb length, and that the difference exceeds the within-group divergence (Tables 3 and 4). This is probably one of the most valuable parts of the investigation. It is not as important to note that head and tail portionalities are similar as to note that the latter reinforce and substantiate the fundamental toe and color pattern differences.

Summary

Amphiuma has been separated into two species, *Amphiuma means* and *Amphiuma tridactylum,* by Baker on the basis of number of toes, color and the ratios of total length to body length and body length to limb lengths. In deriving the mean ratios, Baker did not recognize the influence of ontogenetic variation, allometric growth or sexual dimorphism.

This writer's research was concerned with the evaluation of the three assumptions above and an attempt to determine the real differences between the two-toed groups and the three-toed groups.

Heretofore, *Amphiuma* has been separated into a maximum of three groups to be compared with each other. Goin divided *Amphiuma* into a three-toed group, a two-toed group and an intergrade group and compared these groups. The author divided 537 *Amphiuma* into six series on the basis of geographical distribution. Series 1 is composed of individuals collected west of the Mississippi River; Series 2 consists of individuals from Audubon Park; Series 3 includes those individuals within the alluvial valley east of the Mississippi River; Series 4 (three-toed) and Series 5 (two-toed) includes those *Amphiuma* within the region where the alluvial valley of the Mississippi River meets the East Gulf Coastal Plain; Series 6 is composed of individuals from the Atlantic coastal states.

The reason for this division of *Amphiuma* into series was to determine the range of variation within the three-toed series and within the two-toed series so that the differences between two-toed and three-toed *Amphiuma* could be interpreted more accurately. The Audubon Park series was separated from all other series because it is geographically isolated and the individuals of this series do not reach a size as large as those from the surrounding areas. Since it was not known whether or not the three-toed *Amphiuma* within the eastern alluvial valley of the Mississippi River were genetically similar to those west of the Mississippi, these two series were separated. Series 5 was separated from Series 6 in order to determine if there was any difference between these two two-toed groups and to determine if there was a closer relationship between Series 5 and Series 6 than between Series 4 and Series 5.

The characters used in determining the differences and/or similarities between the series are number of toes, coloration, body proportions of head length to body length, fore-limb length to body length, hind-limb length to body length and tail length to body length. The two-toed and the three-toed *Amphiuma* cannot be completely

separated into two groups by any one of the above characters. The best separation is obtained on the basis of number of toes and throat coloration.

Intergradation is indicated in only three specimens out of 131 from the critical area (Series 4 and 5). On the basis of this investigation the three individuals are considered hybrids. The indication of species separation is further reinforced by the fact that three-toed individuals, as a group, differ from the two-toed in proportionate limb length, and that the difference exceeds the within-group divergence.

Acknowledgements

I am indebted to Dr. Fred R. Cagle of the Department of Zoology, Tulane University, for suggesting this problem and for many helpful suggestions during the course of this study and the preparation of this manuscript. I am indebted to Drs. E. S. Hathaway and G. H. Penn for their critical analysis. For the loan of specimens, I wish to thank Mr. Charles M. Bogert of the American Museum of Natural History, Dr. Doris M. Cochran of the United States National Museum, Mr. Richard Etheridge of Houston, Texas, and Dr. Arnold B. Grobman of the University of Florida. Mr. Allan H. Chaney and other graduate students at Tulane University were helpful in collecting additional field samples after this research was begun.

References Cited

Baker, C. L. 1945. The natural history and morphology of amphiumae. *Jour. Tenn. Acad. Sci.*, 20: 55-91.

_____ 1947. The species of amphiumae. *Jour. Tenn. Acad. Sci.*, 22: 9-21.

Brimley, C. S. 1909. Some notes on the zoology of Lake Ellis, Craven County, North Carolina, with special reference to herpetology. *Proc. Biol. Soc. Wash.*, 22: 129-137.

Cagle, Fred R. 1948. Observations on a population of the salamander, *Amphiuma tridactylum* Cuvier. *Ecology*, 29: 479-491.

Cope, E. D. 1886. Synonymic list of the North American species of *Bufo* and *Rana*, with descriptions of some new species of Batrachia, from specimens in the National Museum. *Proc. Amer. Phil. Soc.*, 23: 514-526.

Cuvier, M. Le Bon 1827. Sur le genre de reptiles batraciens, Nomme Amphiuma, et sur une nouvelle espece de ce genre (*Amphiuma tridactylum*). *Mem. Mus. Hist. Nat. Paris*, 14: 7.

Fisher, R. A. 1938. *Statistical Methods for Research Workers*, (7th ed.). Oliver and Boyd, London, pp. 1-356.

Fitzinger, Leopoldo 1843. *Systema Reptilium, Fasciculus Primus Ambyglossae*, 106, IX p.

Goin, C. J. 1938. The status of *Amphiuma tridactylum* Cuvier. *Herpetologica*, 1: 127-130.

Hubbs, Carl L. and Clark Hubbs 1953. An improved graphical analysis and comparison of series of samples. *Systematic Zoology*, 2: 49-56, 92.

KLAUBER, L. M. 1938. A statistical study of the rattlesnakes: V. Head dimensions. *Occ. Pap. San Diego Soc. Nat. Hist.*, No. 4: 1-53.

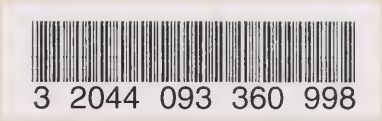
_____ 1941. Four papers on the application of statistical methods to herpetological problems. *Bull. Zool. Soc. San Diego*, No. 17: 5-71.

_____ 1943. Tail length differences in snakes with notes on sexual dimorphism and the coefficient of divergence. *Bull. Zool. Soc. San Diego*, No. 18: 1-60.

PEATMAN, JOHN G. 1947. *Descriptive and Sampling Statistics*. Harper and Brothers, New York, pp. 1-577.

RYDER, JOHN A. 1880. Morphological notes on the limbs of amphiumae, as indicating a possible synonomy of the supposed genera. *Proc. Acad. Nat. Sci. Phila.*, 1879: 14-15.

STEJNEGER, LEONHARD and THOMAS BARBOUR 1943. *Check List of North American Amphibians and Reptiles* (5th ed.). Harvard University Press, Cambridge, pp. 3-4.


3 2044 093 360 998

Date Due